L.M.B.C. MEMOIRS

XXIX.

HALIOTIS

Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY
JAMES JOHNSTONE, D.Sc., & R. J. DANIEL, M.Sc.

XXIX.

HALIOTIS

BY

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(With 8 Plates)

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EDITOR'S PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Forty-two Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the seashore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible station at Port Erin in the centre of the rich collecting grounds at the south end of the Isle of Man. A larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902. In 1920 the Committee ceased to exist and the management of the station was transferred to the Oceanography Department of the University at Liverpool. The name "L.M.B.C. Memoirs" is, however, still retained.

In these forty-two years' experience of a Biological Station, where University students and amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with

by specialists. The same want has probably been felt in other similar institutions and in many University laboratories.

The objects of the Department and of the workers at the Biological Station are chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Department hopes in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following is a list of the Memoirs now published:—

Memoir XXII. ECHINODERM LARVÆ, H. C. Chadwick, 40 pp., 9 Pls., 2s. 6d.

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„ XXVIII. SAGITTA, S. T. Burfield, 112 pp., 12 Pls., 6s. 6d.

„ XXIX. HALIOTIS, Doris R. Crofts, 182 pp., 8 Pls. (2 col.), 10s. 6d. [The Editors acknowledge, with many thanks, a contribution of £50 towards the cost of printing this Memoir from the Publications Fund of the University of London.]

OCEANOGRAPHY DEPARTMENT,
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NOTICE

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INTRODUCTION.

THE name *Haliotis*, meaning "sea-ear," was given by Linnæus, in 1740, to this Gastropod genus with ear-shaped shell.

These molluscs, widely distributed on granite rocks in tropical and temperate seas, are much sought after because of their decorative shells and the food value and delectable quality of the soft parts. At one time they made a staple food for many savage nations. There are now thriving *Haliotis* fisheries in California, Japan and, on a smaller

scale, in the Channel Islands. The visceral mass and mantle fringe are removed and the foot and epipodial muscles are cut into steaks. After suitable pounding they are cooked; in some parts of the world the slices are dried in the sun, after partial cooking, but in California they are canned for American and Chinese markets.

C. L. Edwards reported in 1913 that the "abalone" (*Haliotis*) fishery of California is likely to develop to one of great value. At Long Beach in 1912 "abalones" made 95,800 dollars.

In 1850, Johnston quotes Kaempfer's "History of Japan," which describes Japanese women diving for the esteemed "awabi" (*Haliotis gigantea*). They go down armed with darts to defend themselves. "They pull off the 'Awabi' suddenly before the animal is aware, because otherwise . . . . no force would be strong enough to tear it off."

The beautiful shells are used for jewellery, lamp shades, paper knives and for inlaying purposes. In Siam they serve for spoons and rice dishes. Edwards, in 1913, and Boutan, in 1923, suggested the use of *Haliotis* for cultivated pearls. In *Haliotis tuberculata* I have found small free pearls, which have been produced naturally.

Well known edible species are *H. tuberculata* Linnæus, of Europe; *H. gigantea* Chemnitz, of Japan; *H. rufescens* Swainson, and *H. cracherodii* Leach, two of the five species of California and the East Indian Islands.

Haliotis tuberculata is of considerable economic importance and is met with in the fish markets in the Channel Islands under the popular name "ormer," a contraction of "oreille de mer." "Ormers" are gathered at the extreme spring tides of November to April and are sold at about fourpence each.

T. A. Stephenson, in 1924, published some notes on *Haliotis tuberculata*, based upon his three months' investigation for the Guernsey States, concerning the reason for

the serious diminution of "ormers" off the shores of that island.

The Guernsey States adopted his suggestion for two years' suspension of "ormering" (1924-26) but it is yet too early for recovery in numbers to be obvious. I think that permanent reservation areas would produce lasting increase in the "ormers." On the neighbouring islands of Alderney and Brecqhou and the rocks of Burhou, Ecrehos and Minquiers, "ormers" are still so abundant that one can easily obtain fourteen dozen at low tide of good spring tides.

On one occasion, in 1927, I estimated the catch of a party on one small beach as 1,750. Stephenson, therefore, is doubtless correct in his view that overfishing and disturbance of rocks bearing the seaweed food of *Haliotis* is mainly responsible for the shortage in Guernsey. Fortunately the part of the beach inhabited by "ormers" is only partially exposed at low tide during about seven tides in the year. The prohibited season appears to cover the spawning season, but this should be more strictly enforced.

Since 1898 a Guernsey "ordinance" has forbidden the gathering of, and import or export of, "ormers less than 3 inches in largest diameter."

SYSTEMATIC POSITION AND AFFINITIES.

Haliotis belongs to the sub-class Streptoneura of the Gastropoda. The Streptoneura exhibit torsion of the visceral mass, resulting in the visceral nerve cords crossing into a figure of eight.

The Aspidobranchia and Pectinibranchia are the two orders into which the Streptoneura are divided. In the Aspidobranchia the maximum amount of torsion is found, the ctenidia are usually anterior to the heart, and bilateral symmetry is partly retained, whereas in the Pectinibranchia the nervous system shows concentration, all traces of bilateral symmetry in the viscera are lost,

and the gonad has developed an orifice separate from the renal organs.

The Aspidobranchia are sub-divided into the Docoglossa, with few strong radular teeth, including *Patella* and *Acmæa*, and the Rhipidoglossa, with numerous marginal teeth, including *Pleurotomaria*, *Haliotis*, *Fissurella* and *Emarginula*. This sub-division is, however, open to criticism, for there is no sharp division between the two sub-orders, both of which have primitive genera that have changed little since Silurian and Cambrian times. In some respects the Rhipidoglossa are less specialised than the Docoglossa and show more of the original bilateral symmetry in the ctenidia, auricles, osphradia and hypobranchial glands. As in Lamellibranchia, the ventricle encloses part of the intestine. Specialisation is shown in the presence of a well-developed epipodium, a pallio-visceral anastomosis (dialyneury) and in the radular teeth.

Perrier, 1889, suggested division of the Aspidobranchia (Diotocardia) according to the characters of the renal organs, but this is also unsatisfactory.

The Haliotidæ (Fleming) is a family belonging to the Zygobranchia, a section of the Rhipidoglossa in which there are two bipectinate ctenidia directed anteriorly after larval torsion so that the respiratory chamber lies immediately behind the head. Professor Garstang, 1928, has pointed out, in the early post-larval creeping phase the head prevents exit of waste water in the middle line. All members of this most primitive section (Zygobranchia) have consequently developed a mantle slit in the morphological middle line of this chamber and a corresponding slit, hole or perforations in the shell to allow for separation of the outgoing deoxygenated water and excretory current from the incoming respiratory current.

The Haliotidæ, Scissurellidæ and Fissurellidæ are closely related and, according to Garstang's views on " The

Evolution of Larval Forms," 1928, all the genera included in these families repeat the ontogeny of *Emarginula* until after the outset of adult life, when the shell slit is converted into a hole or into a series of perforations. These differing modifications of the shell slit probably provide for a different problem in oxygenation and " sanitation " in each genus concerned.

In the Haliotidæ the respiratory cavity is displaced to the left side by the enormous development of the right shell muscle. There is a row of shell perforations on the left side lying over the long mantle cleft, near the base of which anal, renal and genital products escape and pass mainly through the shell pores with the " spent " water current. The holes are successively obliterated as new holes form at the shell margin. Mantle tentacles clean the open shell holes. The ctenidia are placed symmetrically on either side of the anus and are washed with fresh water, when the shell lifts, along the whole free anterior and right border. The right ctenidium shows slight reduction. The family is also characterised by marked flattening of the visceral mass and shell, with great reduction in the spire, so that the animal consists mainly of the last visceral and shell whorl. The shell aperture is relatively enormous. *Haliotis* shows many of the archaic features of the Aspidobranchia. The original bilateral symmetry is retained in the heart and the excretory and respiratory systems. There is complete torsion of the mantle cavity and shell through 180°. The nervous system is very primitive in having a long labial commissure, several anterior anastomoses and the pedal ganglia in the form of long anastomosing cords. The eye is open, as in Trochidæ and Stomatellidæ, although Rhipidoglossa generally have a more highly specialised closed eye.

The family is further characterised by the enormous development of the epipodium, which bears a profusion of sensory structures.

Haliotis (Linnæus) is the single genus of the family, with two sub-genera, *Teinotis* and *Padollus*. There are seventy-five species.

Haliotis tuberculata is the only species occurring on British Coasts (Channel Islands) (see Geographical Distribution). It is distinguished by rugosities of the shell and a region of profuse tubercles between the epipodial fringes.

SUITABILITY FOR DISSECTION.

Haliotis tuberculata is worthy of a detailed account written in English because it is the only primitive British Gastropod which is large enough for satisfactory dissection. In specimens of marketable size the shell may be 12 cm. in length, and the extended living animal may have a length of 20 cm.

Many interesting archaic features in Gastropod anatomy are readily demonstrated in *Haliotis* and in some of its less primitive characters it is interesting from the phylogenetic point of view. Streptoneury is clearly shown, but it is difficult to dissect the pedal nerve cords because of the hardness of the pedal muscles after fixation. Special methods must be adopted. (*Vide* Nervous System directions.)

SCOPE OF THE PRESENT WORK.

Throughout this work, the somewhat contradictory statements of previous authors and new details have been checked in both living and preserved specimens.

The only two original figures of the external features hitherto published are by Cuvier, 1817, and Fleure, 1904. Cuvier's figure gives an inaccurate representation of this beautiful Mollusc and Fleure's dorsal view is inadequate.

The general anatomy is not completely figured by any one author.

There is much contradiction in the work of former authors as to the details of the blood vascular system,

nervous system, buccal musculature, excretory organs and reno-pericardial canals. I have endeavoured to clear up the doubtful points. Particular attention has been paid to the previously undetermined details of the multiplicity of sense organs which are so characteristic of *Haliotis* and are evidently important structures in relation to its mode of life.

A good deal of the bionomical information is new. There is also new work on the cytology and physiology of the digestive system, excretory system, lymphoid tissue and mucous and shell-forming glands.

MATERIAL AND METHODS.

Most of the animals used were *Haliotis tuberculata* from the Channel Islands of Brecqhou, Sark, Jersey, Ecrehos, but some specimens of *H. lamellosa* from Naples, and of *H. cracherodii* from California, were also used.

A good deal of the histological and experimental work was done during Easter and Summer Vacations (1926-28) on Brecqhou, an island of 160 acres close to Sark. The one-housed island was particularly convenient for bionomical work and I am much indebted to Mr. Sharp for constructing small concrete barracks at the low-tide limit. In addition, crab-pots and boxes sunken to the normal depth for *Haliotis*, were used for animals undergoing physiological experiments. The only difficulty was the absence of usual laboratory facilities.

For serial sections specimens ranging from only 2 mm. to 30 mm. in length were preserved in various ways after narcotising from twelve to twenty-four hours with menthol crystals. Portions of older animals were also sectioned. The best results were obtained after fixation in Bouin, Flemming (without acetic), and Carnoy (saline sublimate), but the last gave " artefact " pigments. Unfortunately silica and granite fragments in the alimentary canal sometimes caused tearing of sections. It was therefore necessary to cut many series. Neutral red, Janus green,

methylene blue and trypan blue were used for vital staining and for physiological injection.

For dissection specimens are best preserved in equal parts of 90 per cent. alcohol, 2·5 per cent. formalin (in sea-water if possible) and glycerine. The glycerine prevents the usual hardening and contraction of the massive muscles of the shell and foot. To ensure special expansion of the epipodial and other sensory structures the animal may be narcotised with menthol, or by Lo Bianco's method, but this is not essential for a general dissection. Maceration in potassium bichromate or in Béla Haller's mixture is helpful for dissection of the pedal nerve cords. (See Nervous System.)

M. le Cocq, Crown Villa, Trinity, Jersey, will supply *Haliotis tuberculata*. The animals will carry from Jersey or Guernsey unpreserved and wrapped in seaweed ; but it is preferable to send jars with preserving fluid. The shells should be removed immediately on arrival. (See directions on p. 29.)

Specimens of *H. rufescens* and *H. cracherodii* can be obtained from the Pacific Biological Laboratories, Pacific Grove, California ; *H. rufescens* may be 25 cm. long. It is advisable to request the removal of the shell prior to preservation.

I am much indebted to Professor F. J. Cole, F.R.S., to Mr. C. Tate Regan, F.R.S., and to Professor Ashworth, F.R.S., for advice. My thanks are also due to my sister for help with the drawings of living *Haliotis*, to Dr. Esdaile for the loan of apparatus, to Dr. T. A. Stephenson for the loan of sections for comparison, and to Mr. R. J. Daniel, Dr. H. A. Baylis, Dr. Nellie Eales and Mr. G. C. Robson for helpful suggestions.

My thanks are also due to the Committee of the Publication Fund of the University of London for a grant in aid of publication.

HISTORICAL SUMMARY.

The " sea-ear " is mentioned, in the fourth century B.C., by Aristotle in his " Historia Animalium." He correctly supposed that the shell perforations allow for escape of excretory matter. The same animal is also referred to as " big Patella " and " wild limpet." In his translation (529*b*, 15), D'Arcy Thompson says the last name is " commonly attributed to *Fissurella graeca* and conceals a forgotten name for the sea-ear, *Haliotis*."

Belon, however, in 1553, calls attention to Aristotle's reference to " the other *Patella major* " under the name " *Aporrhais*." In his " De aquatilibus " he gives probably the earliest published figure of *Haliotis*. It is an inside view of the shell, with five holes " through which " (he imagined) " it admits and expels water," and is named " the other Patella major."

In his " De Piscibus Marinis," 1555, Rondelet has the second published figure of the shell of *Haliotis*. It is an external view and bears the inscription " De Oreille Marine."

In Sprat's " History of the Royal Society of London for Improving of Natural Knowledge," 1667, reference is made to " clacas," of Teneriffe, which " is absolutely the very best shell-fish in the world, they grow in the rocks five or six under one great shell, through the top holes whereof they peep out with their Nebs." Johnston, in his " Marine Conchology " says he cannot make out what Sprat's " clacas " may be. The " top holes " suggest the perforations of *Haliotis*, through which the mantle tentacles emerge.

In 1681, Grew, in the " Catalogue of Rareties of the Royal Society," First Edition, states that the sea-ear is " found in abundance near Garnsey (Guernsey) Island " and, quoting Lister, he says " The Goldsmiths in France beautify cabinets with split plates."

The name *Haliotis* appears to have been first given by Linnæus, in 1740, in his "Systema naturæ," Ed. II. He distinguished nineteen species (*Vide* Louis Agassiz, 1842-46).

Cuvier, in 1817, wrote the earliest recorded anatomical account of *Haliotis* in his "Mémoires pour servir à l'histoire et à l'anatomie des Mollusques," containing "Mémoire sur l'Haliotide, ou Oreille de Mer; sur le Sigaret, etc." There are several good figures, but there are errors, particularly in the nervous system. His description is brief.

In 1843, Lamarck mentions the external features of *Haliotis* and in 1846 Lebert described the buccal organs but made no remarks of special interest.

The valuable work of Milne-Edwards, in 1847, on the "Circulation chez les Mollusques (Voyage en Sicile)" contains good figures of the circulation of *Haliotis*, which are the foundation of the few more recent accounts of the lacunar nature of the cephalic part of the arterial system in *Patella* and *Haliotis*.

Lacaze-Duthiers (1859) published a masterly and very detailed account of the nervous system of *Haliotis*, and in 1872 he described the "otocysts" of *Haliotis* and other Gastropods. His account of the double nature of each of the pedal nerve strands, with his lengthy application of this as evidence that the epipodium is of mantle derivation, was based on faulty observation and is the one serious error in the work. Cuvier made the same error.

In 1881, Spengel corrected this mistake in his "Geruchsorgan und Nervensystem der Mollusken."

B. Haller's comparative anatomical work, 1883 and 1886 and 1894, has some good figures, which do not agree with some of the seriously inaccurate statements he makes. Wegmann's contribution to the anatomy of *Haliotis*, in 1884, is particularly helpful in relation to the circulation and the digestive system. He repeats

Lacaze-Duthiers' error about the nervous system without attempting to verify microscopically. His work is not intended to be a complete monograph. He particularly emphasises the affinities of *Haliotis* with Lamellibranchia.

Perrier, 1889, Kowalevsky, 1889 and 1894, Cuénot, 1891 and 1899, and Pelseneer 1896 and 1898, published comparative work on the renal organs of Mollusca with specific mention of *Haliotis*. They dealt with the histology, excretory rôle and phagocytic activities of the renal organs, using the method of physiological injection. The works of Kowalevsky and Cuénot are also concerned with the blood and lymphatic glands of Mollusca. Their results are conflicting, particularly with regard to the much modified left renal organ (papillated sac) and there are confused ideas concerning the genital organ in Rhipidoglossa.

A number of other works on comparative anatomy and phylogeny, published during the nineteenth century, make reference to the gonad and renal organs of *Haliotis* and are listed under "Literature." They give conflicting ideas concerning the genital and renal organs of Rhipidoglossa.

Extremely little work has been done on the development of *Haliotis*. Boutan's "La cause principale de l'asymétrie des Mollusques Gastéropodes," published in 1899, described the trochosphere larva and development of the shell of *Haliotis*. He was unable to determine at what age metamorphosis takes place.

In 1902, Totzauer and Fleure published papers on the relations of the renal organs of *Haliotis*.

The only comprehensive description of *Haliotis* is that of Fleure, published in German in 1904. In this useful account he amends the observations made on the renal organs in 1902 and discusses the phylogeny of *Haliotis*.

BIONOMICS.

Habitat and Geographical Distribution.

Haliotis tuberculata is benthic and dwells in the deeper parts of the littoral zone and in the shallow water zone of the sea to an undetermined depth. Joubin, quoted by Stephenson, says it extends only a few inches below low water of "springs," but off Brecqhou Island we obtained odd specimens in about seventeen fathoms in July, 1927. They are certainly very abundant under 30-40 feet of water at low water of spring-tide, for blasting of the rocks from this depth during the construction of Alderney breakwater threw up vast numbers of *Haliotis*.

They are available for abundant collection only from clean rocky beaches at low water of extreme spring tides. This represents in the Channel Islands a fall of 28-30 feet.

Exceptionally they are found in favourable lagoons at higher level, where there is sufficient volume of water to prevent much heating by the sun. Stephenson states that Orton and Sinel have also found them in similar situations.

Haliotis tuberculata is very abundant where the conditions are suitable, but it needs ideally aerated clean water of suitable temperature and salinity. My observations at different times of the year support Stephenson's remark that it is impossible to keep full-grown ones in carefully renewed still water more than twenty-four hours in the summer. They live longer in still water in March and are probably more susceptible to changes of temperature and salinity than to erratic aeration.*

Minute "ormers," 2 to 10 mm. in greatest diameter, however, will live and grow as long as 4½ months in a bowl with daily changes of water.

Haliotis is absent wherever there is much sand, which would interfere with respiration and would hamper the

* Stephenson noted that Flattely and Walton quote experiments by Beudant, in 1816, showing that *Haliotis* is unusually susceptible to lowering of salinity.

growth of the more delicate seaweeds on which it browses. The animals are generally found on the under surfaces of rocks and stones, which are too large to be lifted without difficulty and too heavy to be moved by the waves.

They prefer darkness and frequently cram themselves into very small spaces. It may be partly because of this habit of seeking darkness under stones that they are unable to thrive higher up than the Laminarian zone, for the greater force of the breakers there would move the boulders and crush them. It is interesting that only odd spawning *Haliotis* were found on the upper surface of boulders. The smaller "ormers," 2 mm. to 7 mm. long, are often attached under smaller stones in deeper water in protected gullys and it is only possible to find them at exceptionally low tides. Probably this is why Stephenson found no animals smaller than 9 mm. long, during the summer. When the tide ebbs from the animals they remain quite still and retracted as much as possible, but they start to creep at the turn of the tide before the water approaches near enough for surface tension to affect them.

The geographical range of *Haliotis* is in temperate and tropical seas, but the genus is only abundant in warmer waters. The most northern limit is in Asia at Petropavlovsk; In America the northern limit is possibly Alaska*, and in Europe the northern limit is Alderney and Cherbourg. The southern limit is the subantarctic islands of New Zealand, and the Macquarie Islands. It is also found near Capetown.

Haliotis tuberculata is the English Channel species. It is found wherever the coasts are rocky around the Channel Islands, French and Brittany coasts, as far north as Cherbourg. *Haliotis lamellosa* is the closely related Mediterranean species, which has distinctly marked growth

**Haliotis kamschatkana* Jonas, 1845, of Kamchatka Sea, Alaska to Redondo, California, and Sendai, Japan. Thompson, 1920, after earnest search failed to find this in British Columbia and Alaska. He states that Point St. George, for *H. rufescens*, is the northernmost record, but "abalones" are never abundant in N. California.

ribs. Other species are widely distributed in Japan, China, the Malay Archipelago, America, Australia, New Zealand and South Africa. *Haliotis gigantea* and *H. cracherodii* frequently attain twice the length of *H. tuberculata*.

FOSSIL REMAINS.

The strong shell of *Haliotis* is well suited to preservation. Fossil forms are known from the Cretaceous period and onwards. They appear in the African Chalk (Maastricht) and are frequent in European Miocene and Pliocene.

FOOD.

The early writers ascertained that *Haliotis* is phytophagous. It "browses" on a variety of seaweeds. Stephenson and others have noticed that in captivity its feeding is mainly nocturnal. I watched tiny ones feeding on luminescent weed at night. Probably they are active in the daytime when normally covered by some feet of water. Mature animals show preference for the delicate Algæ, particularly red seaweeds such as *Delesseria* and *Griffithsia*, but will eat *Chondrus* as well as coarser weeds. Hydrozoa, polyzoa, sponges, diatoms, foraminifera, etc., are recognisable in the crop contents and also small fragments of granite and sand. These are probably taken in with the seaweeds. Animals only a few millimetres long prefer to eat *Corallina* and *Lithothamnion*, which they resemble in colouring and I have watched them, as Boutan and Stephenson have done, licking up with their radulæ small particles from a glass surface. They probably lick foraminifera, etc., from the surface of stones. (See Method of Feeding with Digestive System.)

ENEMIES.

Empty *Haliotis* shells are frequently found when "ormering." These indicate the ravages of sea-birds, octopods, large star-fish and possibly rays. I have seen black-backed gulls make unsuccessful attempts to remove

" ormers " left bare by the tide ; it is probable that they and " oyster catchers " are sometimes successful at the turn of the tide when the animals normally relax their powerful grip and begin to move. Cooke, in the " Cambridge Natural History : Mollusca," reports an instance at San Diego of *H. cracherodii* trapping a prairie wolf, which was seizing its soft body for food. The shell was found shut tightly over the dead wolf's nose. Edwards, 1913, reports that two Chinese fishermen were drowned because their hands had been caught by the " abalones " for which they were diving off California. Possibly man is the most serious enemy of *Haliotis*, which he gathers for its commercial value.

PARASITES.

I have found no record of parasites of *Haliotis*. Out of over four hundred *Haliotis* examined at different times of the year, many of which were put back into the sea, only two showed noticeable disease of the soft parts, although the shells were frequently damaged by boring organisms such as *Lithodomus* and *Pholadidea*, and regeneration may produce various abnormalities in the shell. In August, 1926, a full-grown female *Haliotis* was found in a much shrunken condition. When the shell was removed almost the whole surface of the visceral mass, mantle, mucous glands and ctenidia were orange in colour, owing to infestation by a Trematode. Sporocysts, rediæ and cercariæ were present. The last were very active, having a contractile tail with a collared appearance when contracted.*

It is possibly a new species, somewhat resembling *Cercaria brachyura* Lespes, recorded in 1912 by Lebour, on *Gibbula cineræ* as a species new to Britain. The cercariæ on *Haliotis* differ from this in the characters of the suckers

* Total length 0·4 mm. ; diameter of oval sucker 0·04 mm., and of ventral sucker 0·02 mm. ; latter half-way towards tail ; excretory vesicle very large and lined with very large cells.

and tail and it is hoped to make further investigation of them.

The other "sick ormer," a male, was found in April, 1926. Numbers of "cysts" were present between the digestive gland and the testis. Dr. H. A. Baylis very kindly examined these. He suggested that they are Haplosporidian capsules.*

When sectioned the balls contained in the capsules are dotted masses of protoplasm. Dr. A. P. Jameson, Protozoologist to the Cambridge Institute of Animal Pathology, says the cysts have the appearance of a Haplosporidian prior to spore formation and unfortunately all the "cysts" examined are in the same condition.

PROTECTIVE RESEMBLANCES.

The animal, in its normal habitat on the under surfaces of rocks, is so suitably disguised that discovery is only made by the practised eye. Animals under 1 cm. in length have protective colouration very different from the larger *Haliotis*, but in each case there is unmistakable resemblance to the surroundings. The minute ones are coral-pink, mottled with grey and white—a convincing imitation of the *Lithothamnion* and scattered *Spirorbis* so abundant on the under surfaces of grey granite rocks found at the extreme limit of low tide. The soft parts of tiny *Haliotis* are almost transparent, and have very delicate shades of green. The black pigment of older animals has not yet developed. The bulky older animals resemble larger parts of their surroundings. The shells are grey to red, according to the type of rock in the neighbourhood and are often encrusted by various epiphytic growths, mainly *Balanus*, *Spirorbis*, *Anomia*, and various polyzoa and sponges; sometimes an algal growth covers so evenly that it seems to be the natural surface of the shell. Usually, however, the epiphytic growth is not bulky, but one inactive old *Haliotis* was discovered

* Caullery and Chappellier, 1906, *Compt. rend. Soc. Biol. Paris*, Vol. LX, p. 325. Haplosporidian in Trematode of *Donax*.

in a lagoon with a garden of fourteen kinds of seaweed on its shell.

The massive muscular plaque of the foot and epipodium, with its wealth of sense organs, cannot be accommodated inside the shell, so they assume protective resemblances. When irritated they contract as a rigid collar round the shell, with hard knobs resembling rugosities on a rock surface. These are richly pigmented. There are alternating light and dark pigmented areas with white specks on the dorsal surface of the foot and the ventral and dorsal surfaces of the epipodium. Soft green, brown, light grey and black pigments intermingle. The shell also has alternate light and dark markings and the tentacles are vivid green. The entire effect is a camouflage of rugged granite surfaces with attached seaweeds, *Spirorbis*, etc.

My simple experiments on the effect of different coloured lights on "ormers" in captivity showed that they invariably shun white light and are not affected by red light. They are found in dark crevices on the under side of boulders, so that it seems unlikely that the tegumentary pigment is caused by the effect of light on the skin, as Fleure suggested. Possibly the "liver" selects pigment from the seaweeds eaten to use it again. Fleure is probably correct in the view that the pigment protects the delicate parts against light rays.

The flat saucer-shaped shell has probably developed to accommodate the animal to life in rock crevices.

FIXATION TO ROCK SURFACE.

"Ormers" are usually found suspended from the under surfaces of rocks with their weight supported by the attachment of the large area of the cream-coloured pedal sole. Fair-sized animals weigh 8 ounces. When the hypertrophied mass of muscles in the foot and shell muscle are in a state of tonus, due to irritation of the animal, it is easier to tear the shell from the animal than to release the foothold. It is only possible to remove it by leverage under

the side of the sole. Probably, therefore, a good deal of the clinging is due to a vacuum. When adhering to a glass surface the sole is spread over as large an area as possible. Some contraction is then seen and irregular patches of the pedal sole are lifted from the glass, producing small vacua. Larger vacua are made when the animal is irritated. Mucus, exuded by the glands of the foot sole, hardens in water and helps in the early stages of adhesion and is particularly important in tiny animals, which have an additional anterior viscous foot gland.

The state of tonus lasts but a short time if the animal be left alone. When the animal begins to stir it is easily removed if quickly seized.

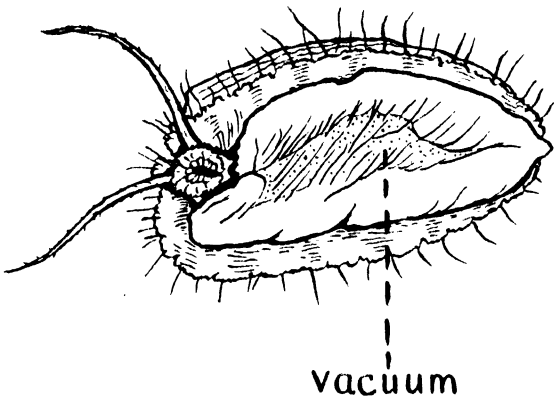
CREEPING.

Haliotis is usually very active and the firmness of its foot tissues aids vigorous action. Tiny ones in captivity creep very energetically at night over seaweeds and to fresh stones, but in the daytime they seldom leave the rock surface.

Specimens between 3 cm. and 5 cm. greatest diameter of shell travelled distances varying from 8 to 20 inches per minute, when timed by stop-watch. Rough estimates of the rate of progress of larger specimens have been previously given as varying from 15 to 20 feet per minute, but in this distance there would be many stops and the rate is probably more like 20 to 30 inches per minute. In a finger bowl and in small rock pools the small animals persistently travel in a sun-wise direction, i.e., continuing in the dextral direction of the spiral of the shell. There is probably less resistance to progress in this direction because of the steady lowering of the height of the shell towards the right side. Large "ormers" fit themselves into extraordinarily small crevices between rocks, wedging this anterior right-hand part of the shell into the narrowest part.

As in the snail the pedal-sole locomotion can be watched

through glass. The waves of contraction can be seen, though less distinctly than in the snail. The two lobes at the anterior end of the foot move alternately and rhythmically (Text-fig. 1). The lobes contract alternately, lift slightly, stretch and make fresh contact. Like the snail, *Haliotis* " slides " on its own copious secretion of mucus, and progression is helped by expansion in parts of the foot due to blood flow into the large lacunar spaces. A slight swinging of the shell and contained visceral mass from side to side by the columellar muscle seems also to aid progression.



TEXT-FIG. 1. Ventral view of young *Haliotis*—to show alternate movement of lobes of pedal sole during creeping. ×1.

When detached specimens, from the heaviest to the lightest, are placed on their backs (fig. 2), they are able to turn over quickly, even out of water. In preparation for turning, the foot and epipodium are swung violently by the shell muscle through about 180°. This is repeated until the outstretched epipodial tentacles and other sense organs of the epipodium and of the dorsal surface of the foot, find a possible surface for adhesion. Then the pedal sole is turned down as far as the mobility of the parts will allow, and as soon as a small portion of the clinging epithelium has adhered, the powerful foot and columellar

muscles work in conjunction and heave the body violently over (figs. 3 and 4). Usually the posterior end commences the feat, but it is sometimes done from the anterior end. The dorsal foot groove does not seem to cling as Fleure supposed, and is not essential for turning over. It may be mainly to allow for cleaning of the space between the dorsal surface of the epipodium and the viscera (cf., the diagonal track mentioned with the respiratory cavity). The ability to turn over must be very useful to *Haliotis* when it falls from weeds or from the ventral surfaces of rocks.

As has been previously mentioned, *Haliotis* leaves no scar on the rocks as limpets do, and, as Stephenson noted, it will creep over encrusting organisms. It is far more difficult to determine their " comings and goings " than with limpets, for marked specimens can only be hunted for at low water of spring tides.

I marked a number of *Haliotis* with silver wire and celluloid tags, and also the rocks to which they were attached. In only two instances were the animals ever seen again under the same rock. Two very large specimens were under an immovable shelving rock. They were evidently well established in this favourable situation, for they were " at home " at two successive spring tides in March and April, 1927, and again in July and August, 1927. My impression is that " homing " in *Haliotis* is exceptional.

GROWTH RATE.

The smallest " ormers " we collected varied from 2 mm. to 11 mm. in length of shell. On April 4th, 1927, seven specimens found at one " ormering " tide measured from 2 mm. to 4·5 mm. Their open perforations varied in number from two to three and a half, while the total number of holes, including secondarily closed ones, varied from two to seven and a half. In August, 1927 (5th to 16th), eleven minute *Haliotis* varied from 6 mm. to 10 mm. in length, while on August 6th, 1928, five specimens were from 2·5 mm. to 10 mm. Hitherto specimens had not

been collected smaller than 9 mm. in length, and this was considered exceptional. It seems possible, from the position in which I found the small specimens, that previous collectors had not worked at sufficiently low tides. Four of the specimens collected in April, 1927, were kept in large bowls with plenty of suitable growing seaweed and water changed daily. Three of them died. One on April 4th measured 4 mm. in greatest length and had a total of seven and a half shell holes, four of which had been closed in turn as they became useless with the gradual forward growth of the respiratory cavity, and on July 27th measured 9·5 mm. in length. It had made four new shell perforations and was extremely active. On August 13th of the same year the same animal measured 11 mm. and had made twelve and three-quarter holes in all, of which nine had successively closed by this time. Therefore, there was a total length increment of 7 mm., so that it had nearly trebled its length in 130 days. The width increment was 4·5 mm. and five and a quarter perforations had been added.

Nearly four hundred animals, varying from 6 mm. to 11·5 mm. in length, were measured and labelled with silver wire with celluloid numbers through the perforations, in an attempt to get further data concerning the rate of growth. Only twenty-one specimens were found again after three and a half months, when they had an average increment of 2·6 mm. to their greatest length and 1·5 mm. to their width. Only one labelled specimen was found after a lapse of a year. On August 24th, 1926, it was 21·3 mm. by 15·3 mm., and on July 29th, 1927, it was 33 mm. by 23 mm., and twenty-nine perforations in all had been made, seven of which remained open. The increments were 11·7 mm. and 7·7 mm. respectively, and five holes were new. Concrete barracks in the Laminarian zone were not found satisfactory, as seaweed for food did not grow well and consequently the growth of these

animals was much less than of those outside. It is only possible to make suggestions from these isolated cases. Specimens measuring from 10 mm. to 37 mm. are very common both in spring and summer; the still smaller ones are probably equally common in deeper water and there are no marked gaps between the size groups. This points to a lengthy breeding season. Possibly only the period from December to March is excluded and the tiny animals found in spring may be from spawn of late autumn of the previous year, and the equally small ones of the summer may be from spring spawn, those of the previous autumn and summer spawning having grown perhaps to between 10 mm. and 20 mm. Those measuring 30 mm. to 40 mm. in spring and summer may be two years old, as growth probably gets progressively slower after the first few months. Stephenson thought those measuring from 20 mm. to 39·5 mm. in summer were one year old, and that summer is the breeding time. The evidence for both views is, of course, inadequate. (See also Reproduction System.)

GROWTH RELATION IN "EAR-SHELLS."

In 1926, Sasaki recorded the growth relation between the shorter and longer diameters in *Haliotis gigantea*, in *H. gigantea* var. *mekai*, and in *H. gigantea* var. *discus* at places in Japan varying in temperature. He took the ratio in the last narrower variety at Omoi as the mean (71·29) and he reads his results to show that high temperature may produce narrower shells in the same variety.

In *Haliotis tuberculata* of Brecqhou (Channel Islands), the ratio is 68·7 for two hundred and eighty specimens of marketable size. Therefore, they are narrower than *H. gigantea* var. *discus* at Omoi, and the ratio is nearly the same as at Asamushi. In small *Haliotis tuberculata*, varying from 5 mm. to 50 mm., the shells are wider but the ratio is not constant.

EXTERNAL FEATURES.

(Figs. 1 to 7, and 12.)

Plate I shows seven views of living specimens of *Haliotis tuberculata*. The extremely few figures of the external characters of *Haliotis* previously published give no true idea of its handsome appearance and its movements. As Pelseneer, in 1920, remarks, the figure by Deshayes, after Cuvier, reproduced in Fischer's "Manual de Conchyliologie," p. 844, is obviously imaginary and inaccurate. It is, however, used by Simroth, Taf. II, fig. 2, and others with all the errors of Cuvier's Fig. 9, Pl. I, which shows mantle tentacles protruding from all shell perforations and omits the characteristic closing of unused holes. His figure is manifestly inexact, but it has been used in most text-books.

The exposed soft parts are heavily pigmented with green, brown and black. This gives a colouration that harmonises with the surroundings. Probably the pigment serves as protection from strong light and perhaps also it strengthens the integument.

1. **Tentacles.** The large number of vivid green tentacles projecting far beyond the shell is the most striking external feature.

(*a*) *The Cephalic Tentacles* (*ceph.t.*) are the two longest and stoutest, and can extend quite an inch long in "ormers" of marketable size, but are relatively longer in small animals. A fine dorsal longitudinal dark brown stripe passes nearly to the tip.

(*b*) *Three Small Pallial Tentacles* (*mant.t.*) pass through the shell holes and are borne around the edge of the mantle cleft. There are never more than three of these tentacles (in one specimen the posterior one was absent), although Cuvier figures about sixteen for this same species. Usually the posterior one at the base of the pallial cleft is through the oldest open hole, and the other two may be through

any of the younger perforations. They frequently change their position and occasionally two are through one hole. Pelseneer, 1920, says they pass through the first three orifices. When in movement they appear to be engaged in keeping the holes clean for the outlet of the respiratory water current (figs. 1 and 5). It is unlikely that they aid in the formation of new shell holes as Fleure suggests, for they are never seen at the shell margin.

(*c*) *The Epipodial Tentacles* (fig. 6, *ep.t.*). The epipodium is more elaborate in *Haliotis* than in any other Gastropod. It is a collarette arising from the dorsal part of the foot and stretching laterally from the cephalic tentacles to the posterior end of the body, where it is interrupted by the colourless dorsal foot groove already mentioned. The numerous sensory structures, other than the epipodial tentacles, are pigmented black, brown and green. Dorsally and ventrally the epipodium has a scalloped fringe fairly rhythmically cut by larger and smaller notches (*ep.d.f.* and *ep.v.f.*). The tentacles are lodged in the larger notches. Notches and tentacles are particularly numerous on the ventral fringe. The intermediate portion is an area of grey-black hillocks bearing knobs (*ep.h.*) with black gulleys and small green tentacles between. This intermediate area of sensory structures is characteristic of *H. tuberculata*. *Haliotis gigantea* and *Haliotis iris* have only the two scalloped fringes with a cleft between. Further details are given with the description of the sense organs.

2. **Cephalic Region.** This region can be withdrawn under the shell for protection. It carries the snout, the cephalic tentacles and the stumpy eye protuberances, between which stretches a small sensory head pleat with notches (*ceph.p.*). The snout is conical and very muscular, but is in no sense a proboscis (fig. 4, *sn.*). The mouth is a depressed dorso-ventral slit, bordered by ridges and papillæ. The cleft anterior end of the foot allows free movement of the mouth, but the anterior foot lobes and

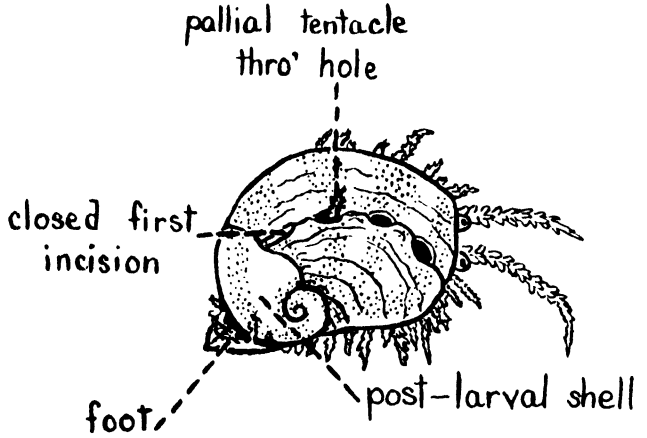
neighbouring parts of the epipodium can completely cover and protect the snout and mouth.

3. **Foot.** This relatively large muscular disc has an extensive ventral creeping surface, which is cleft anteriorly and pointed posteriorly (*ped.so.*). It gives a large surface for adhesion, but at the same time is mobile and suited for rapid progression. For the colour of its various parts see " Protective Resemblances."

4. **Shell Muscle** (figs. 4 and 5, *sh.m.r.* and *sh.m.l.*). There are two shell muscles but the right one is hypertrophied and is placed centrally. It is usually spoken of as " the shell muscle " or " columellar muscle." When *Haliotis* is creeping beneath a shelving rock or when turning over it is obvious (fig. 5). It rises up as a stout muscular pillar from the centre of the muscular plaque of the foot and epipodium and is inserted in the centre of the shell. The large scar left by it is seen inside the shell, as also is the scar of the very small left shell muscle (fig. 7).

5. **Shell** (fig. 7). The shell is large and is remarkable for the extreme smallness of the apical spire and the extraordinarily large last whorl (body whorl), which is much depressed so that it has a relatively enormous aperture. The left margin is inflexed but the right margin is simple. As already stated, this saucer-shape has probably evolved from a taller spire because of the habit of squeezing into confined spaces between rocks (see Protective Resemblances). This flattening results in inability to retract completely into the shell. An operculum would therefore be useless and is missing except in the larva (Boutan). *Haliotis* relies on its resemblances to its surroundings and its great adhesive powers for protection. The shell is secreted by the margin of the mantle and its thickness is increased by growth from the whole mantle surface, enclosing the flattened visceral mass. Only the minutest coil of the visceral mass goes up into the one

spiral turn (fig. 12, *visc.sp.*). The colour of the shell was mentioned with the protective resemblances. As Fleure has suggested, it is probably owing to the habit of crawling beneath rocks, dorsal side downwards, that *Haliotis* has a row of respiratory perforations, corresponding with the cleft line of the mantle over the branchial chamber, instead of a continuous slit, as in *Emarginula*. A slit would allow sand and deposited refuse to collect inside the extensive branchial chamber and impede respiration. Boutan states that the shell commences, as it does in *Fissurella* and *Pleurotomaria*, without slit or perforations and the tiniest attached specimens I have found (2 mm. long) show this original shell marked off by a ridge from the new part of the shell, which has perforations (Text-fig. 2).



TEXT-FIG. 2. *Haliotis tuberculata* (2·5 mm. long) to show post-larval shell with entire margin and added shell with median, first formed perforations. ×13.

The mantle cleft may originate in the post-larval phase by inhibition of growth due to the waste products and deficiency of oxygen in the outgoing respiratory current above the head, as Garstang suggests for most zygobranchs. This cleft, accompanied by a corresponding shell incision,

gives the satisfactory arrangement of separate incoming and outgoing respiratory currents. (See Respiratory System.) The holes are needed only when the ctenidia are well developed. The first holes to appear are nearly in the middle line of the shell. By the time four or five have been formed the body has grown so that the earliest formed hole is now posterior to the mantle cleft and therefore is useless for the outlet of the respiratory current. The older holes are then closed successively with pearly growth secreted by the mantle and new holes are formed at the margin of the shell to compensate for them. They are most probably begun like the shell incision in a young *Fissurella*, by the periphery of the mantle lobes at the tip of the mantle cleft leaving a gap, then approximating again to close the hole (Boutan). The only difference from *Fissurella* is that the process does not cease after one hole is formed but goes on fairly rhythmically to produce a series of holes. This marginal gap between the mantle lobes may be caused by an increase in the volume of the out-going " waste " current (fig. 5, *d.c.*), which is the remnant of the original median current, diverted to the right side by head development ; increase in this current may occur as the respiratory chamber moves forwards with the body growth and the older shell holes become useless. In living specimens with a shell hole in the process of formation this current is most pronounced (see also Shell and Formation of Perforations). The shell margin would be deposited round the edge of the mantle gap until a definite notch would provide exit for a separate vertical outflow of " waste " water, as through the pores. This would improve the separation from the incoming respiratory current (fig. 5). The mantle margins would then become adjacent again and their shell deposit complete the border of the hole. This process would be repeated as soon as another posterior hole became useless.

The shape of the shell changes much with the enormous

development of the right shell muscle, which becomes central and pushes the branchial chamber and corresponding shell perforations to the left side. At the same time the shell grows more rapidly on the right side than on the left. The shell is carried so that the reduced spire lies above the posterior end of the foot, the row of perforations curves along the left side and the latest formed holes lie over the head, pointing towards the cephalic tentacle of the right side.

Ridges radiate from the apex of the spire, curving with the spiral twist and spreading towards the aperture, where the edge has corresponding crenations. Growth marks are at right-angles to these crenations but are often very erratic, owing to weather conditions, epiphytic growths, etc. The rate of growth was measured in isolated specimens. (See Growth Rate.)

TOPOGRAPHY OF ORGANS WHEN SHELL REMOVED.

(Throughout the description the words "right" and "left" refer to the topographical position.)

[Lift the cephalic region and the anterior mantle lobes away from the shell with the flat end of a scalpel. The small left shell muscle and the left double edge of the mantle gripping the shell edge are next easily dislodged, but the massive right shell muscle must be forcibly removed.]

1. **Shell Muscles.** The surface of the right adductor muscle of the shell is seen as a most striking oval white area, which occupies considerable room in the centre of the body (fig. 12, *sh.m.r.*). This figure is of a young animal and the shell muscle is not proportionally so large as in full grown animals.

The left shell muscle is very small and lies to the extreme left side near the anterior end of the mucous gland (figs. 7 and 12, *sh.m.l.*).

2. **The Visceral Mass.** This lies mainly to the left and posterior borders of the large shell muscle. On the left it is in the floor of the respiratory cavity, from the posterior

end of which it curves round the shell muscle and lies flattened on the ventral mantle plate, which is a free sheet between the visceral mass and foot and epipodium (figs. 12, 17, and *T.S.*,—K.). The reduced visceral spire shows only one coil, which is at the extreme posterior part and attaches to the shell spire by a few muscle fibres. It is often a little to the right of the middle line, but in the living animal the whole posterior visceral mass, with the mantle, can be swung by the shell muscle through 180° in relation to the fixed foot and epipodial mass. The visceral mass is made more extensive by a conical appendage running along the right side of the shell muscle (*con.a.*).

The position of the various organs can be determined by differences in colour and transparency, which are partly retained in preserved specimens. In mature animals the conical appendage and visceral spire are covered by the sheathing gonad which is cream coloured in the male and grey-green in the female (figs. 12 and 17, *g.*).

Patches of red, sometimes seen on various parts of the visceral hump, have been taken by Fleure and others to indicate spawning animals. This colour may be found in winter, when the gonad is spent, and it may extend forwards even to the buccal region. From dissections of fresh specimens, one gathers that it is merely due to the colour of the seaweed which has been eaten.

In mature specimens caught during the spawning season a transparent channel about 1 cm. posterior to the shell muscle indicates the transverse passage for fecundation to the right urocœle (fig. 29, *g.o.*).

On the left the gonad overlaps the brown digestive gland (*d.gl.*). Near the posterior end the stomach is not covered by the digestive gland and is blue-grey and transparent (*st.*). Between the digestive and mucous glands the pericardium and kidneys are situated. The left renal organ (*l.ren.*) is very small and lies against the posterior end of the left mucous gland. It is cream coloured.

The pericardium (*pe.*) is immediately posterior to the left renal organ. The auricles are seen through the transparent wall and in living animals it is possible to watch the heart-beat through it. In fig. 12 the pericardium is opened to show the heart. The right renal organ skirts the whole of the lateral and posterior walls of the pericardium. It is much more extensive than might be supposed from the small posterior portion visible (figs. 12, 17, 29, 30, *r.ren.*).

3. **The Mantle.** The large right anterior lobe and the less extensive left anterior lobe of the mantle, with their borders lying against the flatter half of the shell aperture and against the shell perforations, can be seen *in situ* before removal of the shell, if the cephalic region be pressed down (figs. 3-5, *mant.l.l.* and *mant.l.r.*). These lobes are very sensitive and contractile in the living animal. The borders are pigmented with green and brown and on the dorsal edge there is an outer white line and an inner red rim. The left and posterior shell margin is held between the double mantle rim, from the left shell muscle (*sh.m.l.* in fig. 4) as far as the end of the visceral spire (*mant.f.d.* in fig. 5, also *T.S.*,—C, G and K on Pl. VIII). The dorsal flap of the mantle is attached to the shell, which is flanged in this region to give firmer fixation. In the posterior region the mantle lies entirely ventral to the viscera as a flat sheet (fig. 14 and *T.S.*, K, *mant.pl.m.*), over which the visceral hump lies freely. On the left it continues into the ventral integument beneath the viscera.

[Cut the two short strap-like muscles holding the ventral surface of the visceral mass to the dorsal surface of the ventral mantle plate (fig. 14, *mant.pl.m.*).]

The mantle has been pressed into this ventral position by the great flattening of the visceral hump and the delicate dorsal mantle membrane extends only as far as the oblique dwindling edge (*mant.o.* in fig. 12). From here the mantle is attached to the right side of the large shell muscle and forms a sheath completely enclosing the conical appendage of the visceral mass (figs. 12, 14, 17,

con.a. and *mant.o.*). The ventral part of the sheath is continuous with the posterior mantle plate. The conical appendage sometimes falls out after removal of the shell. The mantle has a lateral border with shallow marginal cleft which extends round the termination of the diverticulum and goes anteriorly as the right mantle lobe (fig. 12, *mant.l.r.*). It is attached around the anterior and left border of the large shell muscle and, on its left margin, borders the mantle fissure. In *Haliotis* it is pushed from the median line position of the Fissurellidæ by the enormous right shell muscle, so that it lies far to the left side. The left mantle lobe (fig. 12, *mant.l.l.*) borders the left side of the cleft and from the left shell muscle (fig. 12, *sh.m.l.*) it continues dorsally round the mucous gland, which has a very delicate lateral mantle attachment. The mantle cleft tentacles are already described.

4. **The Respiratory Cavity.** This is a large space extending laterally from under the left edge of the mucous gland almost as far as the large right shell muscle, and posteriorly it is prolonged as far as the left renal organ. When the mantle borders of the pallial cleft are lifted up, two ctenidia are seen slung by supports from the mantle lobes of both sides (figs. 12 and 20, *ct.* and *ct.r.*). Their free tips are seen through the shell holes (fig. 5). Posteriorly they extend beyond the cleft and the right one can be seen through the transparent mantle between the right shell muscle and the mucous gland (fig. 12). To test the water passing to the ctenidia a pair of extensive osphradia is present. These are yellowish grooved swellings, along the anterior border of each ctenidial support.

The anus opens near the posterior part of the mantle cleft (fig. 12, *a.*). Two slit-like openings in the branchial cavity roof on either side of the rectum will be seen when the respiratory chamber is opened. The left one is the opening of the left renal organ, and the right one discharges the excretion of the right renal organ and the genital products.

TEGUMENTARY GLANDS.

Histology and Physiology of the Mantle and its Appendages.

The mantle is a fold of the epithelium covering a delicate layer of loose connective tissue with muscle fibres, numerous blood vessels and nerves.

The mantle epithelium is usually of the pavement type but is pleated at the mantle periphery, where the cells increase in depth. Pigment cells and sensory cells, supplied by the richly branching mantle nerves, are present both on the dorsal and ventral edge. The dorsal border has well-developed gland cells, which are specially active in shell formation. Where the mantle edge is double, on the left side, there is a longitudinal ridge of tall glandular cells clinging to the curled under edge of the shell. These cells presumably produce the thickened flange for firm attachment (fig. 37).

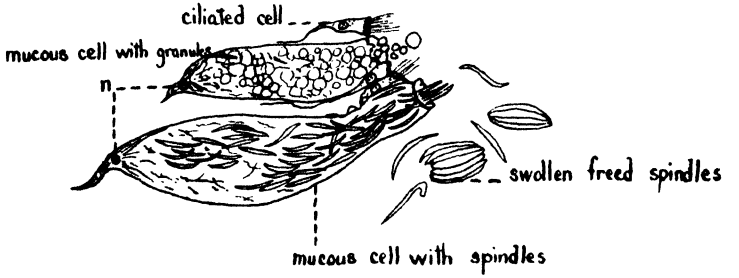
Special developments of the mantle are the mucous glands, the shell-forming glands, the respiratory organs, osphradia and certain patches of lymphoid tissue. The two last will be described with the sense organs and connective tissues respectively.

(*a*) **Mucous Glands** (*Hypobranchial Glands*). The fused mucous glands have already been examined in the dorsal view of the roof of the branchial chamber (fig. 12, *muc.gl.r.* and *l.*).

[Cut along the thin transparent mantle lying to the left of the larger gland and continue cutting round it anteriorly to reach the mantle cleft. Lift up the roof of the respiratory chamber.]

It is now seen that the two mucous glands are attached to the right and left of the rectum, which is covered by the folded ridges of the gland, except for a small section nearest the anus (figs. 20 and 37, *muc.gl.*). The left gland is very extensive, but the right one is only about one-tenth of its size. Simroth says the right is a little

smaller than the left, but Haller denies its existence. Dorsally the division between the two glands is marked by the transparent pallial artery. The glandular epithelium is folded into large pleats to increase the secreting area. The direction of the pleat lines varies. From the glands of the two sides they converge on to the rectum. In the middle and anterior parts of the left gland the deep pleats are almost transverse. The quantity of mucus discharging into the respiratory chamber increases suddenly if the animal is irritated. It is produced for protection and for surrounding and clearing away débris from the anus and renal organs, so keeping the ctenidia clean.



TEXT-FIG. 3. Hypobranchial gland cells (living). ×500.

Histology of the Hypobranchial Glands. While working on living animals, new light has been thrown on the secretory activity of these cells. The tall mucous cells may be 80μ high and are perpendicular to the surface of the pleats. Their nuclei are minute inconspicuous dots crushed near the basement membrane by the mass of secretion, which is stained metachromatically in sections stained with basic dyes. The mucous cells have two types of secretion. The commonest type of mucus is in the form of pointed spindles (Text-fig. 3.). These are packed tightly, side by side, and can be watched passing from the goblet-like opening of the cell, pointed end first and often adhering in bundles. The spindles vary in length from 10μ to 40μ and in every way they are identical

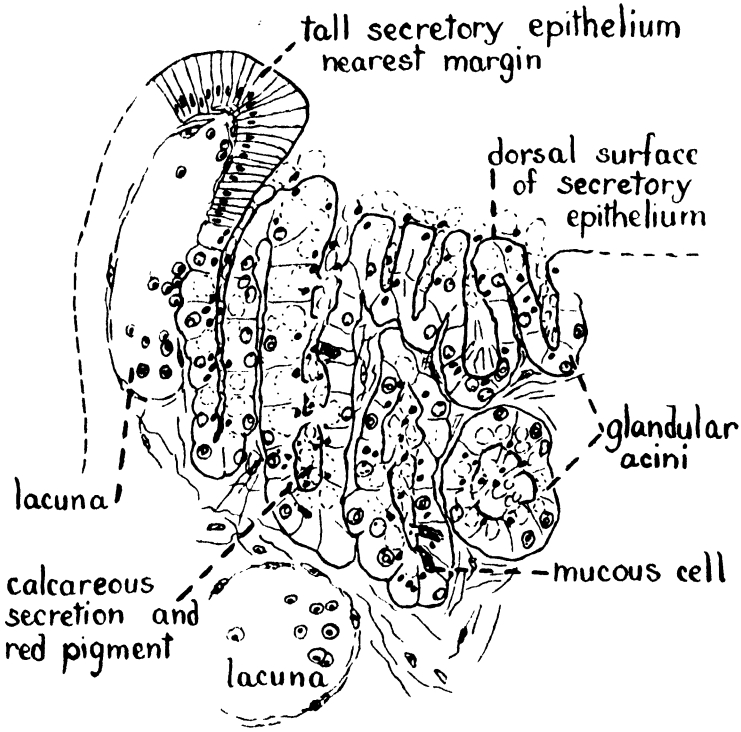
with the "crystals" which Perrier, Cuénot and Fleure interpret as a possible peculiar form of protein food storage found only in the modified left renal organ. The spindles, both from the left renal organ and the mucous glands, however, give positive reactions with microchemical protein tests, because mucin is a glycoproteid. I believe the spindles to be mucin in both instances. The discharged spindles swell up and become indistinct and finally disappear. They stain slightly with methylene blue. These mucous cells appear empty in sections, except for a fine protoplasmic network, because the spindles discharge and swell in the fixing fluid. These gland cells with spindle-shaped secretion are similar to those described and figured by Ashworth in the skin of the cirri of *Scalibregma* and by Eisig and Claparède in a number of Polychæta, but these cells differ from those of *Haliotis* in having pigmented secretion.

Smaller mucous cells, 10μ to 15μ high, with granular refractive contents, lie between the large gland cells. They are of the typical goblet cell type and are possibly young cells, which will develop into the cells with spindle-shaped secretion. They stain deeply with intra-vitam methylene blue and their secretion is precipitated. In sections it stains deeply with mucicarmine (Mayer's solution) which scarcely stains the cells almost emptied of spindle contents. The latter, when living, develop a circular opening for the escape of contents, but the ordinary mucous cells discharge by erratic rupture of the cell wall. Small triangular ciliated cells are wedged between the superficial parts of the glandular cells (Text-fig. 3). Several ciliated cells may lie together. They have long cilia and when finely powdered carmine is scattered over the ventral surface of the pleats of the mucous gland, there appears to be a ciliary current carrying mucus and waste particles along the edges of the pleats towards the mantle cleft, presumably to be discharged through the shell holes.

When a little peppermint, bergamot or aniseed oil is passed through the shell holes of a living animal the mucous glands are irritated and streams of mucus pass out of the shell holes. The mucus is slightly white and cloudy at first, but it soon becomes transparent, unlike that of the foot sole, which solidifies when exposed in sea-water. Probably the spindle-shaped secretion is to facilitate sudden discharge of protective mucus. It is useless for hiding purposes, but in copious secretion it may make the surrounding water objectionable to delicate organisms, which might otherwise attempt to feed on the epipodial decorations. There are scattered neuro-epithelial cells in the mucous glands and running between the lamellæ dorsally there is sparse connective tissue with small arterial and venous channels.

(*b*) **Mantle Glands and Shell Formation.** All parts of the mantle may have shell-forming cells, but the dorsal part near the margin is most active and increases the size of the shell. Other parts of the mantle close the perforations as they become useless, repair damage and add to the thickness of the shell. The portions of the mantle edge most active in shell deposition are an outermost shimmering white line and the rather wider vermilion irregular band, which is most obvious around the anterior edge of the mantle lobes in freshly caught animals. This band has not been described previously. When sectioned it shows simple glandular acini, with much pigment, opening dorsally towards the shell (Text-fig. 4). In fresh teased preparations the pigment is orange to vermilion and is discharging towards the lumen of the acini and there are also large transparent granules. The large nuclei have a distinct nucleolus. The red granules dissolve to a pink fluid in weak hydrochloric acid. They are probably carbonate of lime, highly pigmented with red, for secreting the coloured shell deposit. The colour may be produced by the metabolism in the cells of *Haliotis*,

or it may be selected by the digestive gland from calcareous red seaweeds such as *Corallina* and *Lithothamnion*, which form a considerable part of the diet. In any case the calcareous material is separated from the blood, with which the mantle is copiously supplied, by the mantle epithelial cells. This red marginal deposit forms the



TEXT-FIG. 4. Pigment glands of mantle margin. ×700.

middle coloured stratum of vertical plates (ostracum), but the external white line forms the uppermost thin periostracum consisting of delicate plates of conchin* at right-angles to the middle stratum. The lowest layer (hypostracum) is nacreous and is probably produced by the epithelium of the remainder of the mantle, posterior

* Conchin (C_{80}, H_{48}, N_9, O_{11}) is similar to chitin and only dissolves in hot strong acid. (Halliburton, " Lehrbuch der Chemischen physiologie.")

visceral sac and dorsal covering of the shell muscle. This is absent at the margin of the shell and is very thick towards the centre of good-sized shells. It appears to be formed of membranous layers of conchin in folds and the iridescence is probably due to the surface lineation. The conchin of the periostracum and hypostracum remain, after decalcification, as a delicate transparent shell skeleton which is iridescent. When sectioned *in situ* its layers follow the outline of the body.

Boutan, 1923, in his chapter " L'origine et le mode de formation de la nacre," records his observation of the regeneration of a deformed shell in a young *Haliotis*. The shell was carefully removed and the animal was kept in the aquarium at Roscoff. Only young animals survived the operation. The flexible layer developed first in the erratic regenerated shell. Therefore the pallial epithelial cells secrete periostracum and ostracum when exposed to the water, as around the shell periphery and all over the dorsal surface in the regenerated shell, or in the first development of a shell in embryology, but the same cells give rise to the lamellose mother-of-pearl (hypostracum) of conchin without the calcareous part, when sheltered from direct water contact. Boutan has completely neglected the special marginal vermilion gland; moreover the mantle margin curls up, contracts much and behaves abnormally after the shell removal.

The formation of the shell perforations was mentioned with the external features. The shell bridges between the holes retain a line which corresponds with the line of approximation of the shell-secreting mantle lobes, alternating with their separation to form the holes (fig. 1). I have come across a number of minute spherical pearls embedded in the mantle and between the visceral mass and shell. Pearls have conchin layers like the nacreous lining of the shell, but the lamellæ are concentric and are formed by the epithelium under abnormal conditions. The

necessary inflammation can be produced by fragments of shell, parasitic organisms (Trematodes, etc.) or air bubbles (Mikimoto and Boutan).

Abnormalities of shell in *Haliotis* have been described by Pelseneer, 1920, as instances of continuous and discontinuous variation. The variation in number of perforations is given for *H. tuberculata* and *H. californica*. In individuals of marketable size, of the former species, they vary from four to eight, with six for the majority of specimens. In 194 of my specimens of *H. tuberculata* of marketable size, 101 had six perforations. In *H. californica* they vary from five to nine in young animals and from two to three in the adult.

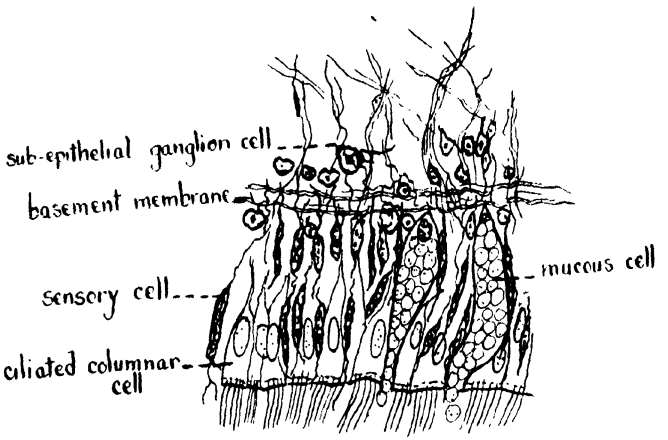
One specimen of *H. gigantea* had a double row of perforations, and odd specimens of four species are recorded with holes entirely absent. I have found one healthy living *Haliotis tuberculata* which was imperforate, although there were closed holes in the older part of the shell. In this case the rectum extended considerably more forward than usual, doubtless to ensure removal of fæcal matter. It is not at all uncommon for the series of holes to be interrupted at various intervals. The rhythm may be broken by mantle injury.

HISTOLOGY AND PHYSIOLOGY OF PEDAL GLANDS.

Small unicellular mucous glands are scattered everywhere in the integument. They are numerous on parts of the ctenidia, as mentioned on p. 49, and are particularly well developed in the foot. The mucous content of these goblet cells appears granular, unlike the spindle form newly described for the hypobranchial mucous glands. The exuded mucus serves for lubrication, for general protection and for healing injuries.

1. **The Pedal Sole** (Text-fig. 5) has abundant unicellular gland cells. These are much elongated and secrete a copious supply of mucus between the pedal sole and the rock surface. The pedal sole progresses by sliding on the

mucus. It is much more viscid than the discharge from the hypobranchial glands and, unlike that, it forms a stiff stringy jelly after exposure to sea water. This helps in the early stages of adhesion. There are abundant ciliated columnar cells and sensory cells. The former

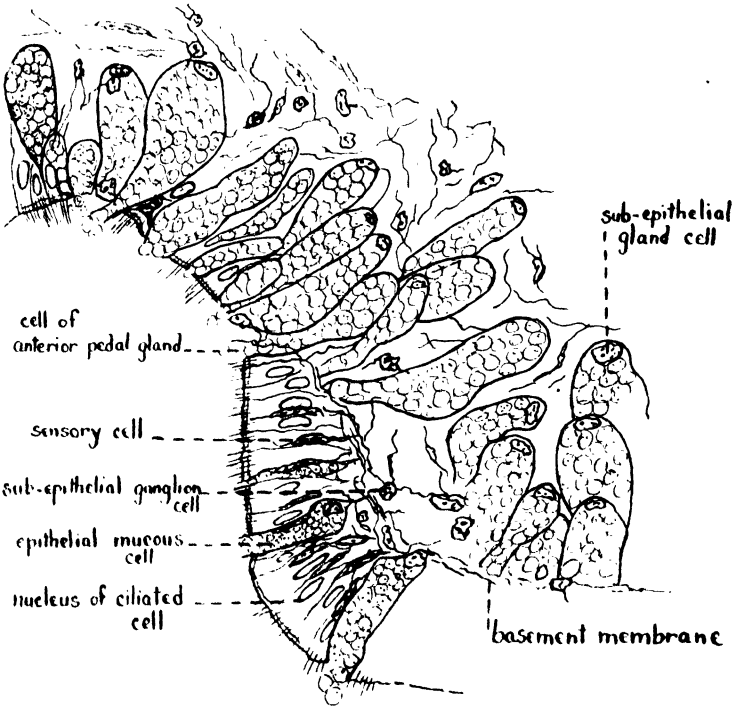


TEXT-FIG. 5. Pedal sole epithelium. ×1,000.

keep the mucus moving but the latter have long processes penetrating to the exterior, short processes connecting with the glandular cells and processes to the sub-epithelial ganglion cells. In addition to general sense perception they probably control secretion of mucus.

2. **The Anterior Pedal Glands** (Text-fig. 6) are situated in a special invagination of the epithelium in the anterior notch of the foot. There are sub-epithelial gland cells, but the invagination is present only in the early post-larval life of *Haliotis*. For this reason, Fleure and others have been unable to find it, although Thiele mentioned it. In specimens up to 3·5 mm. long it is well developed, but in specimens 8 mm. long it has almost disappeared. In maximum development the sub-epithelial glands extend backwards for a third of the length of the foot. The anterior gland cells discharge into the invagina-

tion, but the posterior ones open separately to the exterior. The gland cells are very large and flask shaped. They stain erratically with "specific" mucus stains. After picro-indigo-carmine the anterior gland cells are deep indigo, but the posterior gland cells are delicate blue. Their secretion is viscous, like that of the pedal sole in general. There is probably a difference between ordinary mucous and viscous secretion, as Thiele first suggested.

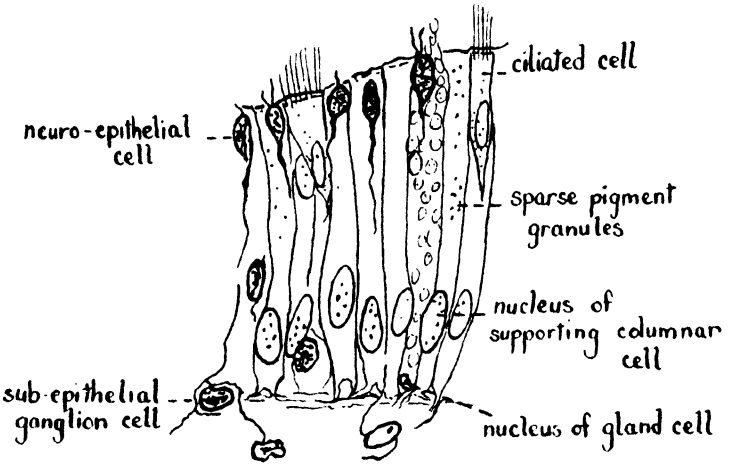


TEXT-FIG. 6. Anterior pedal glands. ×900.

The anterior pedal gland of the very young creeping *Haliotis* doubtless assists in adhesion, for the pedal sole has a minute area and could not produce an effective vacuum.

3. **The Dorsal Posterior Pedal Groove** (Text-fig. 7) is the very noticeable gutter, with lateral grooves leading to it, which lies at the posterior termination of the

epipodium of the two sides. It is cream-coloured like the pedal sole. Fleure stated that it is an additional clinging area, which is used when the animal turns completely over to right itself after having fallen shell downwards. It has been mentioned in the bionomical section that my observations do not support this, but details of the histology of this groove point to a pronounced sensory function and suggest a second function of producing an outgoing cleaning current for the large dorsal surface of the foot and epipodium, which is overhung by the ventral mantle plate. Specks of powdered carmine, caught up



TEXT-FIG. 7. Epithelium of dorsal posterior pedal groove. × 1,000

in mucus, have been observed to pass this way, as they do along the smaller anterior epipodial gutter at the right side of the head. There are few mucous cells in the pedal groove, the columnar epithelium is taller than on the pedal sole and has long cilia. There are numerous sensory cells with processes penetrating among the cilia. In places the neuro-epithelial cells are very near the surface.

When *Haliotis* prepares, by violent twirling of the large shell muscle, for turning back to the clinging position, the

posterior groove is expanded and passed over neighbouring rock surfaces. It appears to "sample" these surfaces but never clings, although the pedal sole of the same region often commences adhesion, prior to the sudden heave over (fig. 3). The wrinkled groove gives flexibility to this region.

RESPIRATORY SYSTEM.

(Figs. 5, 12, 17 and Text-figs. 8, 9, 10.)

The ctenidia (*ct.*) are the special organs of respiration, but the mantle, as in many Gastropods and Lamellibranchs, also takes part in the process. The rich network of its blood vessels, covered only by delicate tissues, makes oxygenation of the blood easy and some mantle blood is carried back to the heart without passing through the ctenidia.

1. Currents of Respiratory Chamber.

The branchial cavity has already been described. Its large size and the great length of the ctenidia provide adequate æration for *Haliotis*, which lives under large stones and rocks. It serves as a kind of cloacal chamber as well as a respiratory chamber and there are special arrangements for keeping a continuous fresh current for oxygenation and for removing waste materials. The respiratory cavity is closed on the left side and posteriorly, but water enters the mantle cavity above the head and along the right side and passes to the respiratory chamber (fig. 5). After bathing the ctenidia the "spent" water, together with most of the excretory and genital products from the renal organs and anus, is shot out of the shell perforations by ciliary action. The outgoing current is aided by pressure of the shell on to the muscular foot and epipodium when the shell muscle contracts (fig. 1). The direction of water currents is watched by dropping powdered carmine in suspension in various positions

near the animal or through the shell holes. The main outlet is through the first, second and third recently-formed perforations. The diagonal current first noticed by Stephenson,* passing off to the right side of the head, seems to remove heavier particles, surrounded by mucin, from the ctenidia and floor of the branchial chamber (fig. 5, *d.c.*). The track of the current is without pigment and runs on the dorsal side of the epipodium close to the right side of the head. It is similar to, but less pronounced than, the dorsal posterior pedal groove. The current is not stopped by holding wet tissue paper flat on the track, which appears to have specially long cilia only in the epipodial region. The current is probably kept going by the long cilia of the ctenidial lamellæ. In living specimens with a shell hole in the process of formation this current is most pronounced. (See also Shell and Formation of Perforations.)

Irritating oils introduced to the entrance of the respiratory chamber seem to be perceived at once by the osphradia, and the shell closes down abruptly. To complete the closing of the respiratory cavity, the mantle lobes come together and block the shell perforations. They are more easily closed than a shell slit, which the probable ancestors of *Haliotis* possessed. When the cavity closes, quantities of mucus are shot out from the mucous glands, perhaps to ensure clearing away of the offending substance.

2. Structure of Ctenidia.

The two ctenidia are bipectinate with equal lamellæ on both sides, unlike those of *Trochus* and *Nerita*. They are attached for about seven-eighths of their length to the mantle, symmetrically on either side of the mantle cleft. They taper to the anterior and posteriorly; their afferent

* T. A. Stephenson, 1924, thought it possible that *Haliotis* could extract plankton as food from this diagonal water current, but he found no growth in animals kept in baskets without seaweed.

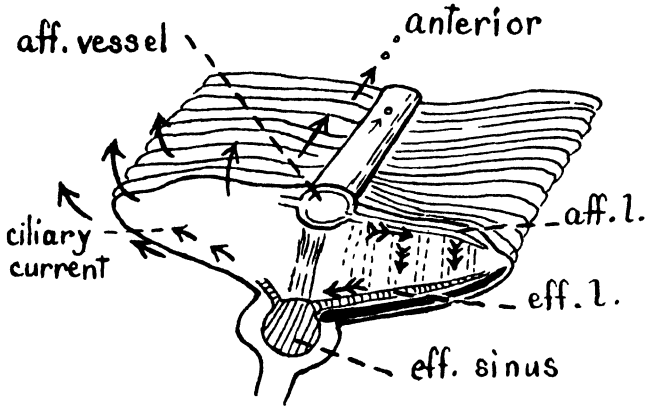
sides are dorsal and the efferent sides ventral (figs. 12, 17, and 36). The left ctenidium is always decidedly larger than the right. This has been used as evidence that the organs on the right side show a tendency towards disappearance, which is characteristic of higher Gastropods, but it is probably the enormous size of the shell muscle, peculiar to *Haliotis*, which has left little room for a larger right ctenidium. In other respects the ctenidia closely resemble those of *Fissurella* and *Incisura*. The left ctenidium is sessile, except anteriorly, where the free tip has a support with an oblique edge. The right one has a special delicate mantle outgrowth supporting it throughout its length. Anteriorly it is thickened and carried out obliquely, as on the left, to the free tip of the ctenidium.

According to Bouvier, 1887, only the free extremity of the ctenidium corresponds to the ancestral gill, and the attached part is a new formation to give better respiration. The osphradium lies along this oblique border (figs. 17, 20 and 35, *os.*). The efferent sinus of the ctenidium lies in the mantle support (Text-figs. 8 and 24, and fig. 17, *eff.ct.s.*), and the afferent vessel runs down the dorsal middle line of the ctenidium (fig. 17, *aff.ct.v.*). The afferent vessels of the two sides pass forward from the basibranchial sinus. Immediately posterior to this there are partitions connecting the afferent sides of the ctenidia with the roof of the branchial chamber at the sides of the renal openings of the respective sides (fig. 38, *T.S.*,—H, *br.p.*). These partitions cut off a small dorsal portion beneath the mucous gland from the more ventral region of the respiratory cavity. As Fleure suggests, this ctenidial supporting partition, feebly developed in *Haliotis*, may be the beginning of the partition extending further forward as in *Trochus*, and dividing the branchial chamber for better oxygenation of the ctenidia. The ctenidia extend into this divided branchial space posterior to the

basi-branchial sinus, which sends a branch to become the posterior afferent vessel (figs. 17 and 29). Half the tapering ctenidial lamellae of this region are in the dorsal half of the chamber and half in the ventral portion.

The rachis and individual ctenidial lamellæ are capable of strong muscular contractions.

Ctenidial Lamellæ. These are vast numbers of outgrowths from the ctenidial rachis. They are delicate, nearly triangular, plates, but with blunt free tips. Text-fig. 8 shows diagrammatically their arrangement

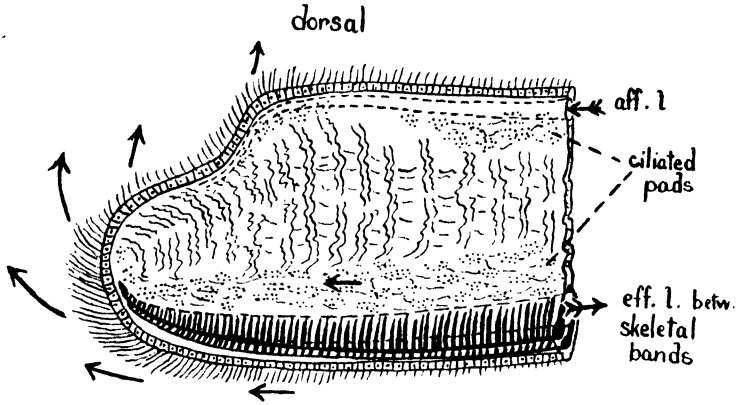


TEXT-FIG. 8. Diagram of arrangement of ctenidial lamellæ. Arrows show direction of ciliary currents on the left and blood-flow on the right.

on the rachis. The base of the triangle is attached dorso-ventrally and at right-angles to the rachis, with each flat anterior surface lying on the posterior surface of the plate anterior to it. The dorsal edges lie at right-angles to the afferent ctenidial vessel and have a lacunar branch from it. The efferent lacunæ are near the ventral edges of the lamellæ and lead into the efferent ctenidial vessel (*aff.l.* and *eff.l.*). The middle region of each plate is transversely pleated to increase the respiratory area (Text-figs. 9 and 10).

Connective Tissue. Beneath the epithelium very sparse connective tissue makes bridging strands between the surfaces of the lamella.

Blood Lacunæ lie between the bridges and there is no capillary system connecting afferent and efferent spaces at the dorsal and ventral edges of the leaf, although Wegmann believed it to be present. The blood streams



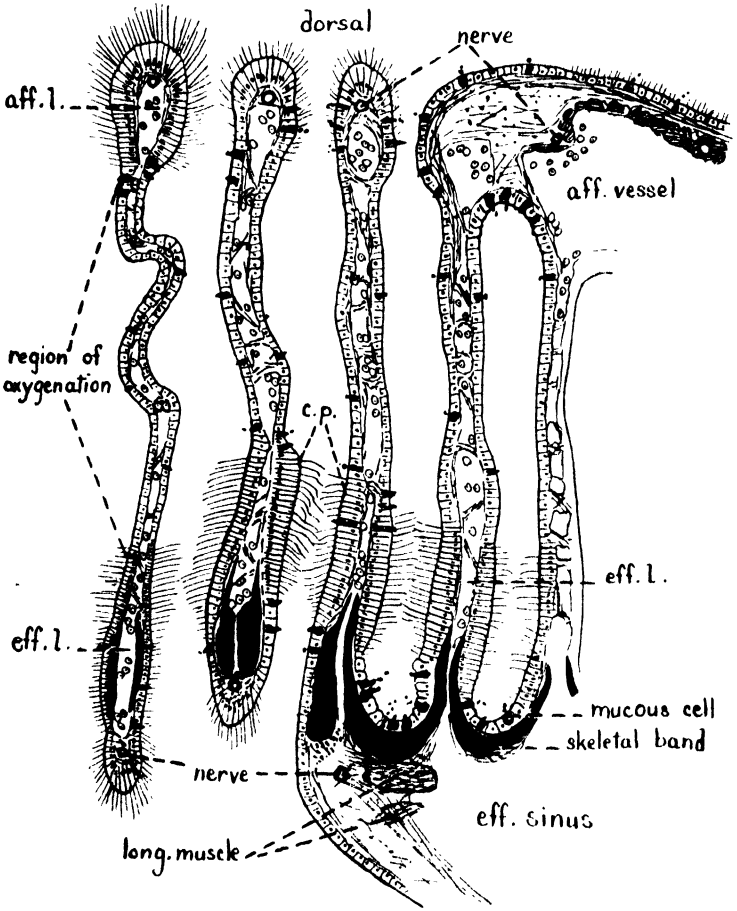
TEXT-FIG. 9. Surface view of ctenidial lamella. Arrows show direction of ciliary currents on left and blood-flow on right.

through the lacunæ between the bridges. Blood collected by the efferent space on the ventral edge has been oxygenated in the pleated middle region, where the lacunæ are half afferent and half efferent (Text-fig. 10).

Chitinous Skeleton. This strengthening is in V-shaped opaque rods with the two limbs of the V in adjacent lamellæ, so that each plate has two bars. Such skeletal bars are present in *Fissurella*, *Pleurotomaria*, *Incisura* and *Trochus*. They are ventral in position and the efferent lacuna is lodged between them. They form a basal support and keep the lamellæ erect, so that water can circulate between. The rods serve also for attachment of muscles which bring about the considerable movements of the plates. They are developed in close relation to collections of cells bearing specially long and functionally important cilia (Text-figs. 9 and 10, *c.p.*).

The Epithelium. This varies much in different parts of the lamellæ. When living lamellæ are cut off they

swim round in sea-water by means of long cilia. The cilia direct the ærating water current between the lamellæ so that water, which has washed the surfaces, leaves at the afferent border and is thrust violently away at the tips



TEXT-FIG. 10. Ctenidium in oblique section, with lamellæ in vertical section to show respiratory arrangements. ×250.

of the lamellæ by extremely long cilia. A region with long cilia extends over the chitinous rod region (Text-figs. 9 and 10). Fleure noticed a ciliated pad in *Haliotis* and also in *Emarginula* and he states that their physiological

significance is to keep the leaves apart for æration by water. The cilia here and at the tip are quite ten times the length of those on other parts. The cells are very tall and narrow and each has one powerful cilium.

Covering the exposed surface of the afferent vessel and the afferent border of the lamellæ, the epithelial cells are tall columnar, mixed with ciliated and goblet cells, but in the central region of each plate the cells are without cilia and low. Patches of glandular cells are well developed near the rachis for supplying mucus for cleaning and lubricating the lamellæ (Text-fig. 10). Sensory cells are scattered throughout the epithelium.

Longitudinal muscle bands are seen on the wall of the efferent sinus. They are attached to the curved part of the V-shaped skeletal rods, but do not penetrate into the lamellæ (Text-figs. 10 and 24). The afferent ctenidial vessel has outer transverse and inner longitudinal muscles, which continue a little into the lamellæ.

The Innervation is separate for the afferent and efferent sides of the ctenidium. The efferent portion is supplied by a special efferent ctenidial nerve of the branchial ganglion. This has a few branches to the free tip of the ctenidium and very numerous branches arise along its course to innervate the longer part of the efferent border of the ctenidium and its supporting membrane (fig. 20, *e.ct.n.*). These were described by Lacaze Duthiers. Simroth states that the afferent side of the ctenidium is not sensory. My observations agree with those of Fleure that there are paired special branches of the rectal nerve passing to the afferent vessels of each side, after giving off a branch to the renal apertures (fig. 20, *aff.ct.n.*). They soon divide into a median and two lateral branches in the wall of the afferent vessel. The sensory and muscle arrangements make the ctenidium highly contractile, so that the delicate lamellar surfaces can be protected.

THE DIGESTIVE SYSTEM.

(Figs. 8 to 11 and Transverse Sections on Pl. VIII.)

The mouth and anus are both directed anteriorly. The forward position of the anus is due to primitive flexure. The super-added Gastropod torsion is shown well in transverse sections of various regions.

Haliotis browses on seaweed, fragments of which it rasps off by the radula, controlled by the odontophore apparatus. The comb-like margins of the radula, assisted by dorso-lateral jaws, allow only small fragments of food to pass into the gut, which has no other triturating apparatus. The acid medium for digestion is supplied by salivary glands.

Most of the gut is incapable of peristalsis, because it is thin-walled, but the contents are kept in motion by cilia. Extra cellular digestive enzymes are provided by extensive digestive glands and probably to a less extent by the stomach cæcum ; the digestive glands are probably also concerned in intra-cellular digestion. The intestine is long and provides a large absorptive surface. Absorption may be aided by phagocytes of the crop, digestive glands, stomach, cæcum and intestine.

[DISSECTION. It is preferable to dissect the superficial parts of the nervous system first, if only one specimen is available. (*Vide* Nervous System Directions.) The respiratory cavity has been exposed by cutting through the very thin transparent mantle along the left border of the mucous gland. Continue cutting the mucous gland from the left renal organ. Pin the pallial roof back to the large shell muscle ; do not remove the mucous gland and mantle unless further specimens are available for the dorsal parts of the nervous system. The thin walled and extensive œsophageal pouches are difficult to follow, if cut open with the integument. Therefore it is best to peel off the integument and oblique muscles with fine forceps. Continue into the head pleat and snout region, between the cephalic tentacles until the cerebral nerve commissure is exposed. Expose the

complete width of œsophageal pouches and continue posteriorly, bearing to the left of the shell muscle until the supra-œsophageal visceral connective is exposed (fig. 20, *visc.co.r.*). Then proceed posteriorly until the visceral connectives are exposed as far as the abdominal ganglion (fig. 20, *abd.g.*). These are directly under the integument and placed laterally to the three regions of the digestive tube of this middle region. The right visceral connective must be cut to complete the dissection. Lift up the intestinal loop (fig. 8, *int.l.*). It turns back upon itself at the anterior end of the shell muscle and when removed exposes the right œsophageal pouch. Next make a median longitudinal incision through the dorsal wall of the œsophagus to expose the lengthy openings of the œsophageal pouches (fig. 8). The radular sac starts ventral to the œsophagus and finishes blindly on the right side of the narrow region of the œsophagus. On the visceral hump the stomach is usually the only part of the digestive canal visible from the dorsal surface, but, when the gonad is small, the spirally coiled cæcum is seen to the left of the visceral spire. (fig. 12, *st.cæc.*) Strip up the gonad as shown in fig. 17, cutting the minute vessels which hold it down. Brush away the genital products from the dorsal parts of the digestive gland, stomach and cæcum. Make a dorsal incision in the stomach, remove its contents and expose the contracted opening from the crop. Continue the incision curving forward and to the left to open the crop. If few specimens are available, omit the intestine region, passing under the pericardium and under the renal organs until the section on the renal organs is reached.]

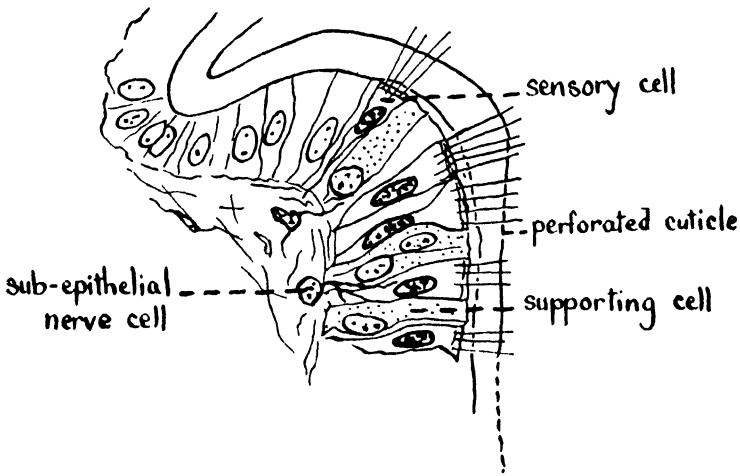
For convenience the digestive organs are considered under four sections :—the buccal region (pharyngeal bulb) with its glands ; the œsophagus with its pouches and dilated crop ; the stomach with its digestive glands and cæcum ; the intestine and anal region.

I. The Buccal Region.

The short cylindrical snout, bearing the vertical mouth cleft, is the only part anterior to the œsophageal nerve ring. This region is slightly curved so that the mouth is ventral. As in other herbivorous forms, there is no invagination to make a proboscis. The odontophore is

a highly muscular mass, which carries the radula forward for browsing. It varies in position in preserved animals. Most of it lies posterior to the oesophageal nerve collar, as is usual in archaic Gastropods. For convenience the buccal cavity is regarded as finishing with the dorsal and ventral valves (figs. 8 and 9, *æs.v.d.* and *æs.v.v.*), although it merges into the œsophagus, which is also of ectodermal origin.

A. **The Buccal Opening** has papillated lips. Several deep longitudinal furrows passing inside the mouth allow for expansion of the mouth and lips. There is thick cuticle, which is perforated for sensory processes of tall sensory cells (Text-fig. 11, and *T.S.*,—A). There are often



TEXT-FIG. 11. Sensory cells (" taste buds ") in transverse section of buccal orifice. ×1,000.

two or three sensory cells together and nerve fibrils can be traced to them. These are the taste buds of Haller, which Fleure was unable to find. The lips have tall sensory, glandular and supporting cells covered with cuticle. The supporting cells have abundant green and black pigment granules. Beneath the snout integument is a stout band of circular muscle and oblique muscles pass into the lip papillæ (fig. 19).

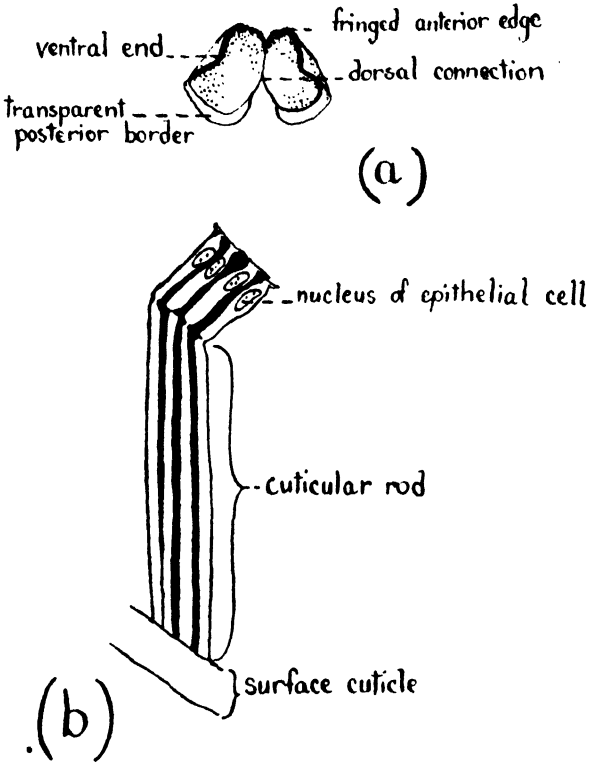
B. **Jaws.** These are amber coloured plates fixed dorso-laterally under the sphincter muscle, so that their edges show when the mouth is open (figs. 8, 18, 19 and 34, *j.*). These immovable chitinous pieces are united dorsally by connective tissue. They give a firm surface for the radula to work against and help to retain in the mouth the pieces of weed it has scraped off. The jaws are developed beneath the ordinary cuticle and the wearing edges break through it. The special buccal cavity epithelium, which secretes them, consists of very regular cells with pale nuclei which have a distinct karyosome. There are spaces between the cells. These " stick cells " secrete very narrow rods perpendicular to the cuticular surface (Text-fig. 12). The prisms are separated into horny filaments by wearing, and are nearly black in large animals.

C. **The Buccal Cavity** (Pharyngeal Cavity) (Text-fig. 15). This is dorsal in position. In its anterior section it is compressed dorso-ventrally by the radular apparatus and the cerebral commissure; behind this nerve it dilates into a spacious cavity, which may bulge over the nerve commissure. Its walls are thin and merge into those of the œsophagus. One pair of salivary glands and a pair of buccal pockets open laterally into it, and a mid-dorsal bulge of the buccal cavity is held over them by muscle strands and nerves (*T.S.*, A,—fig. 34).

D. **Salivary Glands.** These are of the tubulo-alveolar type and are opaque white (fig. 8, *s.gl.*, and Pl. VIII, *T.S.*,—A). They are well hidden at the sides of the buccal mass. The duct is very short and its buccal orifice is in a slight depression under the cerebral commissure, immediately anterior to the buccal pockets (fig. 8, *s.gl.o.*). The glandular epithelium has scanty supporting cells and large goblet cells with basal nuclei. They produce copious acid secretion.

E. **Buccal Pockets.** In the fresh condition these are only slightly less opaque white than the salivary

glands. They are culs-de-sac with long openings puckered with transverse ciliated pads overlying the toothed radular surface. They are larger in *Haliotis* than in related forms and their epithelium is taller than that of the salivary glands. They seem to supplement the secretion of these glands. The secretion may partly dissolve calcareous



TEXT-FIG. 12. (*a*) Jaws in ventral view. ×3.
(*b*) Jaw-secreting cells of lateral epithelium of buccal orifice. ×1,100.

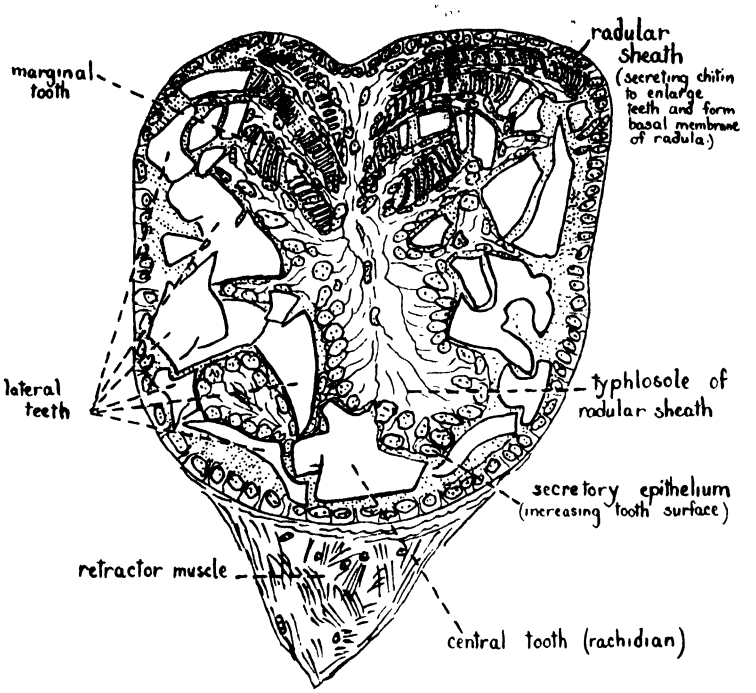
material taken in with food, but is largely responsible for the acid reaction of the contents of the crop and stomach. The cytoplasm of the cells stains with acid dyes.

F. **Dorsal and Ventral Valves** (figs. 8 and 9, *æs.v.d.* and *æs.v.v.*). These point posteriorly into the cavity

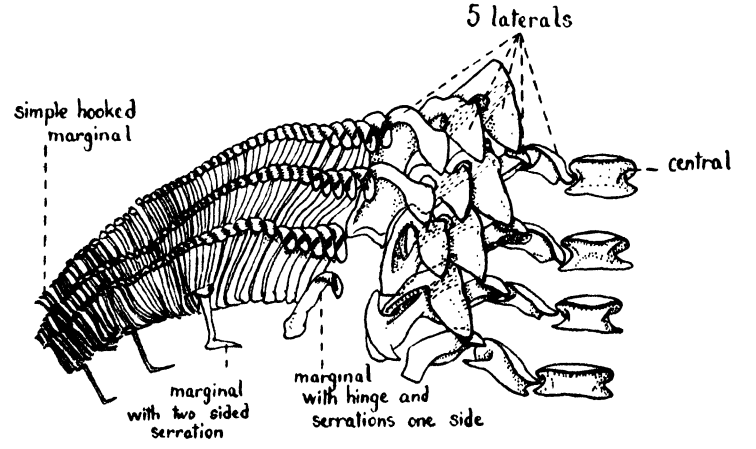
of the œsophagus and prevent reflux of food, which has reached the œsophagus, to the buccal cavity. The epithelium of both valves is ciliated. Anterior to the ventral valve, the floor of the cavity has transverse ridges.

G. **Radula and its Supporting Apparatus** (Text-figs. 13, 14 and 15).

(*a*) *The radula* is large in *Haliotis*. Its position is shown in Text-fig. 15. The edges are rolled in for the posterior two-thirds of its length. The anterior part has the supporting membrane spread to expose the teeth, but it is only exposed in the floor of the buccal cavity as far as the transverse œsophageal fold shown in fig. 8 and Text-fig. 15. From here the radular cæcum is given off ventrally to the œsophagus and its bifurcated blind extremity reaches the narrow region of the œsophagus (fig. 8, *rad.c.e.*). The radular sheath is partly enclosed in the cephalic aorta. The radular ribbon is a cuticular secretion of the epithelium of the basal part of the sheath. The outer parts of the teeth are developed from the sheath epithelium, but the inner parts are developed from a dorsal typhlosole of epithelium (Text-fig. 13). The dorsal intucking has broken down in the part of the radula in use and the organ has opened so that it forms a ribbon. Constant wear of its tip is compensated for by continual growth from the base of the cæcum. The cusps of the teeth are posteriorly directed hooks. The ones in use are brown but younger ones are straw-coloured. Each transverse row is characterised by a large central tooth, while the lateral ones are in three marked series. The marginal teeth are too numerous to count. The radular formula is $\infty . (3 + 2) . 1 . (2 + 3) . \infty$. It is not possible to agree with Simroth that the lateral teeth differ only in size from the stick-like marginal teeth (Text-fig. 14). From the fan-like arrangement of the latter, in the Sub-Order to which *Haliotis* belongs, the name Rhipidoglossa originates.



TEXT-FIG. 13. T.S. of radular cæcum. The epithelium of the typhlosole breaks down for unfolding of radular ribbon. ×450.



TEXT-FIG. 14. Radular teeth of half the ribbon in dorsal view. ×25.

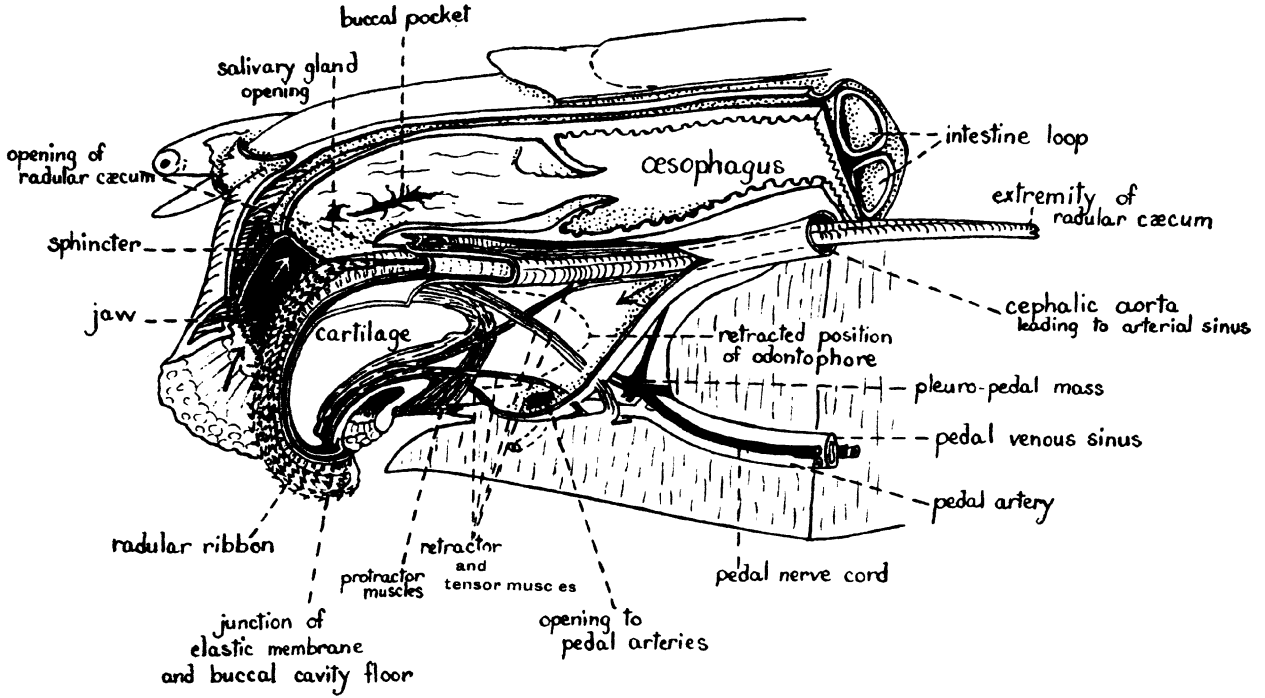
(*b*) *The Odontophore.*

[Lift up the anterior part of the radula to see the dorsal grooved surface of the odontophore over which the radula moves forward when in use. Make an incision in the ventral wall of the œsophagus just behind the origin of the radular cæcum and continue forward through the basal membrane. Lift up the flaps to expose all the dorsal parts of the odontophore. Cut through the snout integument on the left until the odontophore can be rolled up to expose the ventral surface.]

The odontophore apparatus, supporting and controlling the movements of the radula, is a large ventral, almost spherical, mass. It consists of bulky muscles made firm by internal cartilages and covered dorsally by the elastic membrane of the radula. Strong muscle bands attach it to the head integument, to the radular sheath and to the junction of the shell and foot muscles. These control the protraction and retraction of the whole apparatus (Text-fig. 15.)

(i) The Basal Membrane of the Radula. This is a tough transparent cuticular sheath covering the anterior part of the odontophore like a hood. It is cut in the mid-dorsal line in fig. 18, *e.mem.c.* (also see Pl. VIII, *T.S.*,—A). It is an antero-ventral outgrowth of the radular sheath, on which the radula rests. It is continuous with the wall of the buccal cavity.

A ventral protuberance of the anterior hooded part of the elastic membrane is a much smaller longitudinal ridge than in the Fissurellidæ (*T.S.*,—A, *e.mem.r.*). In its anterior part the ridge is gelatinous connective tissue, but a little further back it is fenestrated by a lacuna containing numerous blood cells. Posterior to the insertion of the paired longitudinal tensor muscles on the ventral part of the swelling, the lateral walls of the lacuna break down (fig. 19, R. 18). The ridge seems to make a good insertion for these two tensor muscles of the elastic membrane. Previous authors have said the function of the ridge is problematical.



TEXT-FIG. 15. Diagram of buccal region in median sagittal section, showing lingual apparatus and cephalic arterial and venous sinuses.

(ii) **Supporting Cartilages** (figs. 9, 18, 19 and 34). Dorsally these cartilages form a firm base for the radula and provide fixation for the odontophore muscles. They consist of a large dorsal pair, a small lateral posterior pair and a vestigial anterior ventral pair. The last was discovered by Fleure and is verified in all the animals I have sectioned (fig. 34, *T.S.*,—A, *cart.v.*). Minute vestigial patches of cartilage are found in various parts of the radular sheath. The basal membrane of the radula is closely applied to the dorsal side of the large pair and makes a hood to their tips. They have a median groove to lodge the radula (fig. 34, *T.S.*,—A, *cart.d.*). Thick transverse muscles between their ventral edges widen the groove, when in a state of tonus. The cavity between the cartilages may be filled with blood of the cephalic arterial sinus. The position of the lateral pair of cartilages is seen in figs. 9 and 18, *cart.l.* They provide attachment for intrinsic odontophore muscles and can be brought into more ventral position, thus altering the shape of the odontophore. Gelatinous connective tissue, or cartilage in older animals, attaches them to the dorsal cartilages, which are also fused in their extreme posterior parts. The vestigial cartilages are minute and lie in the mouth region. They are ventral and external to the muscles uniting the dorsal cartilages. They may help to give firmness to the ventral edges of the elastic membrane and jaws. Fleure says they are homologous with the larger inferior lateral cartilages of *Patella*. The skeleton pieces are pearl-white. The "cartilage" has characteristic vesicular structure and resembles fibro-cartilage. The cells are distinct, with clear nucleus and nucleolus and cell division resembles that of true cartilage. The cells are in groups of one to four, with a surrounding layer of hyaline vesicular matrix.

The external parts resemble perichondrium.

(iii) **Musculature of the Odontophore.** The

numerous muscles bring about change in shape, protraction and retraction of the bulb. The complicated movements are concerned in the use of the radula during feeding. The muscles are not inserted on the radula itself, but to its sheath, to the basal membrane, and to the cartilages. The radula participates in their movements. The muscles are very distinctly striped and are flesh coloured in the fresh condition, owing to the presence of hæmoglobin. This is frequently found in Molluscan muscles of special activity, but it has not been recorded previously for *Haliotis*. Because of the great complication of buccal musculature there are considerable discrepancies in the previous accounts. It is necessary to add to the number of muscles previously described (figs. 18, 9, 19, 34).

Extrinsic muscles originate on the buccal wall and have insertions on the odontophore, but intrinsic muscles belong entirely to the radular sheath and odontophore.

The numbers 1-21 are given to the muscles in the order in which they are observed in dissection, starting from the dorsal surface.

Protractor Muscles.

Dorso-lateral Protractors (*P.* 9 and 9*a*). Extrinsic, paired, oblique; origin in lateral head wall; both insertions ventral on lateral cartilage; powerful protractors, also slightly elevating.

Ventro-lateral Protractors (*P.* 10 and 10*a*). Extrinsic, paired, oblique; oblique origin on lateral snout wall; insertions separate on ventro-lateral cartilages; *P.* 10 passes dorsal to cerebro-pleural connectives, but P 10*a* is ventral; powerful protractors.

Lateral Protractors (*P.* 5). Extrinsic, paired, oblique; origin with aponeurosis under lateral head wall, passing dorsal to cerebro-pleural connectives to insertion near base of dorsal cartilage. Tendinous and powerful protractors. (Not previously recorded.)

Ventral Protractors (*P.* 17). Extrinsic, paired, longitudinal; origin on ventral snout wall; insertion mid-ventral on lateral cartilages; powerful protractors. (Not previously recorded.)

Retractor Muscles.

Median Retractor (*R.* 19). Extrinsic, unpaired, ventral, longitudinal; origin in junction of shell and foot muscles; insertion on central posterior extremity of odontophore; most powerful retractor.

Ventral Retractor (*R.* 15). Intrinsic, paired for insertion half; origin on ventral wall of radular sheath posterior to odontophore; insertion on lateral parts of basal membrane, not to its tip as previously recorded; retracts basal membrane and works in conjunction with *R.* 19.

Muscles Controlling Lateral and Tensor Movements of Odontophore. Only slight lateral movement is possible.

Lateral Retractors (*L.* 11). Extrinsic, paired, ventro-lateral, horizontal to oblique; origin inside lateral wall of buccal region; insertion near anterior end of dorsal cartilages; in addition to lateral movements most probably also retracts.

Lateral Retractors (*R.* 1). Extrinsic, paired; origin on ventral wall of œsophagus; insertion on lateral walls of radular sheath at entrance to radular cæcum; retractors of the basal membrane, drawing it tightly against cartilages.

Ventral Tensors (*R.* 18). Extrinsic, paired, longitudinal; origin anterior to shell muscle in muscular sheath surrounding pleuro-pedal nerve mass, course through floor of cephalic sinus; insertion on ventral ridge of elastic membrane; tensors for radular sheath, working over pulley-like gutter between tips of dorsal cartilages.

Lateral Tensors (*L.* 12). Extrinsic, paired, ventro-lateral, horizontal to oblique; origin inside ventro-lateral snout wall; insertion on protuberance of tip of elastic membrane which is turned over to ventral surface; produce lateral movement of elastic membrane to balance lateral movements of underlying cartilages.

Muscles controlling the Radular Cæcum Opening.

Dilatators aiding Retractors (*D.* 1*a*). Small section of *R.* 1; insertion near centre of roof of radular sheath at opening of radular cæcum; origin with *R.* 1; dilatator of cæcal opening to allow radula to be retracted.

Constrictor (*C.* 2). Intrinsic, unpaired, dorsal, horizontal under line of folding of œsophageal wall to form radular cæcum; attached to lateral wall of both large cartilages; constricts opening of cæcum. (Not previously recorded.)

Oblique Dilatators (*D.* 4). Intrinsic, numerous each side, dorso-ventral, oblique; origins along roof of radular cæcum beneath *R.* 1; insertions along lateral and ventral walls of dorsal and lateral cartilages; lift roof of radular cæcum and give form to odontophore.

Muscles shaping Dorsal Surface of Elastic Membrane and preserving Contact of Radula with it.

S. 6. Intrinsic, paired, dorsal, oblique; origin on posterior end of lateral cartilage; insertion central on ventral surface of elastic membrane; preserve contact of basement membrane of radula with under-lying supporting cartilages.

S. 7. Intrinsic, three pairs, dorsal; origin on dorsal surface of large cartilages; insertion beneath elastic membrane; function as 6 and during retraction both sets draw elastic membrane into groove between two large cartilages, making a shallow trough into which radula can drop back. (Not previously recorded.)

S. 16. Intrinsic, numerous, unpaired, ventral, transverse; unite ventral margins of two large cartilages, flatten the bulb by opening the V-shaped groove between the cartilages; work in conjunction with *S.* 6 and *S.* 7, also preserve firmness of skeleton.

S. 14. Intrinsic, paired, ventral, longitudinal; origin on mid-ventral wall of dorsal and lateral cartilages; insertion on ridge in roof of elastic membrane; preserve contact of membrane with underlying cartilages. (Origin first described here.)

Muscles Controlling Shape of Bulb.

S. 8. Intrinsic, three pairs, dorsal, oblique to vertical; attaching lateral cartilages to larger cartilages. (Not previously recorded.)

S. 13. Intrinsic, paired and very numerous, ventral, oblique; attaching ventral parts of lateral cartilages to lateral sides of large ones and mixed with fine muscles to ventral integument.

S. 3. Intrinsic, unpaired, dorsal, transverse; attached to lateral surfaces of both large cartilages, making dorsal posterior band.

Muscles Controlling Buccal Orifice.

Constrictor (*C.* 20). Extrinsic, unpaired, ventral, transverse; attached to lateral walls of snout; helps during protraction by holding up odontophore. (First mentioned here.)

Sphincter (*S.* 21). Thick pad under mouth region of snout; makes supporting pad for jaws and controls position of jaws and size of mouth opening.

The Method of Feeding in *Haliotis* has been described by Fleure, 1904, Boutan, 1923, and Stephenson, 1924. They pointed out that minute encrusting algæ on rock and fragments and surfaces of larger seaweeds are scraped off by the radula; this browsing can be watched with a lens when specimens are feeding on delicate organisms adhering to the glass sides of the vessels in which they are kept. Further details of the process may be added. The cephalic tentacles and the lip papillæ act as selecting organs, the foot and lips give firm fixation for the working of the radula, which has strong lateral teeth for rasping, but the numerous marginal teeth, many of which have a hinge and serrated edges, are obviously too delicate to tear (Text-fig. 14). The hinge of the larger marginal teeth is controlled by stiff hairs, so that the tip can only bend towards the buccal cavity. These teeth probably serve as cogs to help food fragments along and aid the jaws in providing a non-skidding surface to ensure passage of the

fragments into the buccal cavity. In addition they act as combs, working with the jaws to prevent entrance of large fragments. This is necessary because there is no triturating apparatus in the remainder of the digestive system.

I agree with Amaudrut, 1898, and Simroth, 1901, that the slow movements which bring about rasping by the radula are dependent on those of the supporting cartilages, whose action is brought about by the powerful buccal musculature.

When feeding commences, the marginal papillæ and radial grooves of the lips spread flat and cling to the seaweed surface, the central region is lifted and the mouth opens and the tip of the odontophore apparatus is thrust out by contraction of the protractor muscles (fig. 19, and Text-fig. 15). The radula is thrust out with this forward movement of the cartilages because it is controlled by the movements of its underlying elastic membrane, which is an anterior expansion of the radular sheath spread over the anterior ends of the cartilages. The membrane accommodates itself to the movements of the cartilages by its tensor muscles (figs. 18 and 19, *R.* 1, *R.* 18, *S.* 6, *S.* 7, *S.* 14, and *L.* 12), so that the free tip of the radula is drawn over the curve of the protruding ends of the cartilages during protraction and withdrawn into the dorsal groove between the cartilages during retraction. The tips of the radular teeth all point posteriorly when the radula is withdrawn, but when brought into action the seaweed is scraped from a posterior to an anterior direction by the harrow-shaped lateral teeth, which are on prominent lateral ridges, and to a less extent by the gouge-shaped central tooth (Text-figs. 14 and 15). Therefore, as Yonge, 1928, has emphasised for Gastropods generally, the effective tearing action is on the return pull of the apparatus, which is brought about mainly by the large median unpaired retractor (fig. 19, *R.* 19, and Text-fig. 15). The protractor muscles simply

draw the odontophore forward to bring it into position for repetition of the rasping movement of retraction.

The radular ribbon is spread open only when protruded. When not in use the marginal teeth are rolled in, so that their points face those of the lateral teeth, as in the developing region of the radular cæcum (Text-fig. 13). Yonge states that Herrick explains that this prevents self-injury and he believes that in browsing genera the chewing action of the radula working against the jaws continues after actual rasping of food has stopped.

II. Œsophagus (figs. 8, 9, 35 to 37).

The first part of the œsophagus lies dorsal to the radular cæcum. Its opening from the buccal cavity is controlled by the dorsal and ventral œsophageal valves, already described. In fig. 8, *œs.v.d.*, the dorsal valve is shown cut in half.

Œsophageal Pouches. The first section of the œsophagus is very spacious because the small œsophageal lumen is supplemented by the extensive cavities of the œsophageal pouches. They extend to the level of the anus and their internal openings are almost as long, so that they are easily mistaken for the œsophagus itself. The ventral œsophageal wall has numerous gutters and ridges, in inverted **V**-shape. The gutters deepen along the ventral margin of the pouch openings and the right one has extra pleats. The dorsal lining of the œsophagus has irregular curved pleats which are deeper along the dorsal edge than on the opposing edge of the pouch opening. The pouches are lined with minute pointed papillæ. The right œsophageal pouch is most extensive on the right and anterior to the shell muscle, and occupies all the available space left by the buccal apparatus and the intestine loop. It is flattened, as the various transverse sections show. Posteriorly both pouches and œsophagus become narrow and the pouches terminate in blind pockets. Large œsophageal pouches are a common feature in Rhipido-

glossa, but they are particularly large in *Haliotis*. It is curious that *Haliotis* still retains the right pouch larger than the left, as in related families, although the shell muscle causes much compression on the right side.

The œsophagus starts symmetrical with the buccal cavity (fig. 9 and *T.S.*—B). Amaudrut pointed out that twisting in counter-clockwise direction in the adult œsophagus indicates the amount of larval torsion which has brought about the asymmetry of the adult. In transverse sections of *Haliotis* this can be followed by the position of the longitudinal ridges of the ventral surface of the œsophagus, which are replaced by a groove in the narrow section and in the crop. Progress of its torsion to the left is seen in Transverse Sections C, F and H, drawn with the aid of a projection apparatus. In *T.S.*—H, the gutter in the crop epithelium is quite 180° from the starting position of the ventral ridge of the œsophagus wall. It therefore shows the complete torsion, although the presence of this was denied by Fleure.

Œsophageal Epithelium. The epithelium is brown or straw coloured. The tall cells are ciliated columnar, except in the pouches, the papillæ of which have less tall glandular cells with basal nuclei and supporting cells. In contrast with those of the buccal cavity, these cells have basophil contents. The food passes slowly to the crop because of the large œsophageal pouches. This gives time for thorough mixing with the acid salivary secretion.

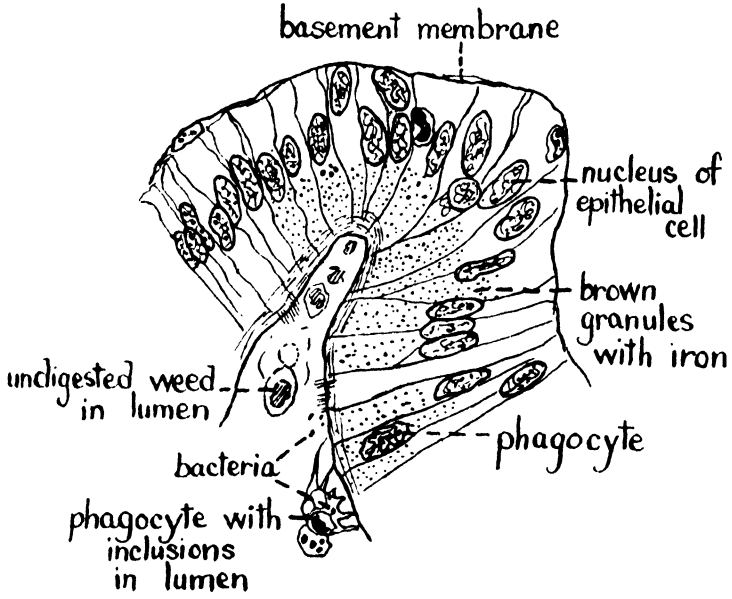
The narrow portion of the œsophageal tube is very short and passes ventrally to both limbs of the intestinal loop (fig. 8, *n.æs.*). Its ciliated epithelium varies from green to orange and suddenly changes to nine or more longitudinal pleats with sharp edges, but the pretorsional mid-ventral line is marked by a smooth gutter. This region has a muscular wall and it probably squeezes the food into smaller fragments to mix it with salivary secretion. There is no triturating apparatus.

The Crop. The canal suddenly widens into this roomy chamber, which was termed "the first stomach" by Cuvier, and "stomach" by Wegmann. It lies ventrally in the visceral mass and is usually hidden in dorsal view by the other viscera. It can be seen through the ventral integument, except during the breeding season, when the gonad hides it (figs. 14 and 38, *cr.*). The right extremity of the crop is a blind pouch resting in the liver and the spiral stomach-cæcum lies over it (figs. 8 and 11, *cr.* and *st.cæc.*). Posteriorly the crop is suddenly constricted by the narrow opening leading to the stomach. The stomach has less than half the capacity of the crop. A semi-circular valve on the ventral and lateral wall of the stomach guards the opening. The crop has a thin wall, but the opening to the stomach is muscular.

The Crop Epithelium. In the fresh state the epithelial lining changes suddenly from orange, in the narrow œsophagus, to grey-green in the crop. The longitudinal pleats of the œsophagus continue as lower pleats right into the crop and additional ones are added as the crop gets larger. The cells of the epithelium are mixed. Tall ciliated and secretory cells are in juxtaposition and intermediate forms may occur; towards the stomach the ciliated cells disappear, giving place to gland cells. Most crop cells have a very oval secretory type of nucleus and the distal half of the cytoplasm has masses of brown-green refractive granules. Specks of iron show up when micro-chemical tests for iron are used. The cells have a darkened band parallel to the surface (Text-fig. 16). Phagocytes are frequent at various depths in the epithelium and free in the lumen. They contain clear vacuoles and particles staining vivid red like bacteria with Unna's Methyl-green and pyronin. The cytology is described differently by Wegmann and Fleure who, however, also disagree. The crop is simply a collecting bag for food and saliva, but its phagocytes may be absorptive.

III. The Stomach.

The stomach extends from the crop opening to the beginning of the intestine, but it is much smaller than the crop. It is called " second stomach " by Cuvier, and " intestine " by Wegmann, while Vayssière figures first, second and third stomachs.



Text-fig. 16. Crop epithelium in T.S. ×1,100.

From the crop opening the digestive tube bends through nearly 180°. The stomach is not sharply marked off from the intestine, but a large pocket valve, which prevents regurgitation, marks the beginning of the intestine (fig. 8, *V.* 3). The stomach has a spiral cæcum which develops late. In *Haliotis* 4 mm. in length it commences as a small simple pouch. There is no crystalline style sac, even in the smallest specimens sectioned. The cæcum receives the secretion from the digestive glands, which have four main orifices placed near the cardiac end

of the stomach. Their curious position is probably due to hypertrophy of the right shell muscle. The two first orifices are actually at the cardiac opening of the stomach and appear multiple because the gland ducts are so short that the secondary openings can be seen (figs. 8, O_1 and O_2). *Fissurella* and *Incisura* also have multiple openings. O_1 leads from the huge portion of digestive gland in the conical appendage and O_2 from the dorsal and ventral portions near the visceral spire. O_2 is more ventral than O_1, and is placed in a very definite gutter, which deepens as it continues a helical course in the spiral cæcum. The right-hand side of the gutter continues forwards to O_1, so that digestive fluid from both openings is directed towards the cæcum. O_1 has an anterior valve preventing its secretion falling into the crop. The two openings together might correspond with the orifice of the right member of a pair of ancestral glands, and the two dorsal openings, O_3 and O_4, leading from the dorsal portions and left conical portion of the digestive gland, might together be the left member of the pair. The dorsal orifices O_3 and O_4, of figs. 8 and 11, are in grooves overhung by valves V_1 and V_2. The latter are very swollen in the fresh state by blood lacunæ of their connective tissues. They hang down and help to close the openings of the crop and cæcum. They prevent large food fragments from entering the cæcum and digestive glands and guide digestive fluid mixed with minute food particles into the cæcum gutter. In the opposite direction this gutter continues along the antero-ventral wall of the stomach and numerous gutters lead from it. Later it transforms into the typhlosole of the intestine. There is an additional groove in the cæcum, posterior and parallel to the first groove, from which it is separated by a longitudinal typhlosole dividing the cæcum cavity into two channels, except at the blind end. The stomach is thin-walled.

Cytology of Epithelium.

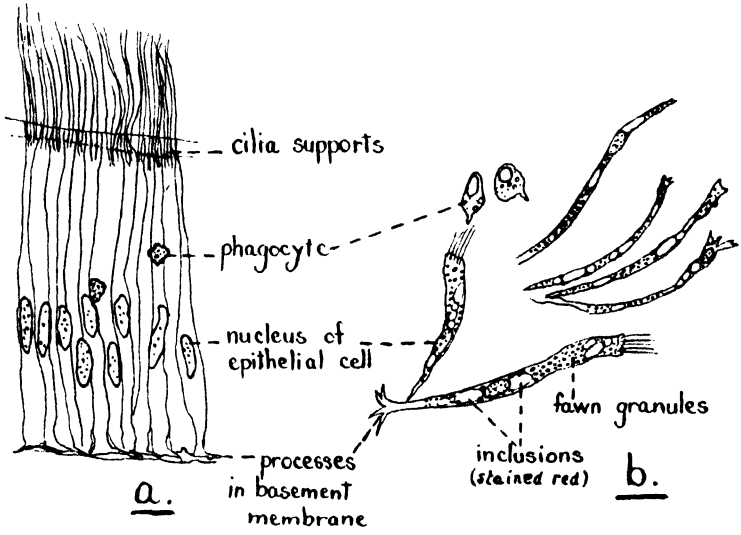
(*a*) *The stomach epithelium* has secretory cells, which are lower and paler in colour than the cells of the crop. The supporting columnar cells have striated borders. As usual there is a caducous cuticle, which may help in squeezing food to mix it with digestive fluid, for the wall is a little more muscular than elsewhere. The cuticle dwindles away near the gutters and the cells are ciliated on the valves and at the entrance of the cæcum and hepatic ducts (fig. 11).

The cilia of these cells are extremely long and the cells are narrowed almost to long threads around the opening of the spiral cæcum. In the gutters there are low secretory cells filled with dense black granules and mucous cells are near the digestive gland and cæcum orifices. The numerous metaplasmic inclusions are acid, unlike those of the crop. Masses of migratory blood cells are in various positions between the cells and at the surface. Their cytoplasm is full of glistening inclusions, which may contain enzymes. They probably function in absorption.

(*b*) *The Cæcum Epithelium.* The epithelium of the thin-walled cæcum is fawn coloured, except for the black pigmented gutters near its stomach opening. The extremely elongated cells, with basal nuclei, are secretory. In the living condition neutral red stains the brown non-living inclusions deep red, but smaller droplets are fawn and alkaline (Text-fig. 17, *b*.). Each cell has a few whip-like cilia, which are especially long on the ridges near the gutters. There are fewer phagocytes than in the stomach and crop epithelium.

Cæcum Contents. There are never recognizable pieces of weed in the lumen, because valves and the narrow orifice prevent their entry. The acid contents are fluid, consisting mainly of golden brown digestive gland secretion, transported to it along the stomach gutters and mixed with minute particles of food surrounded by mucus and acid salivary secretion.

The Digestive Gland. The massive glands arise as extensive diverticula from the stomach orifices. Very brief ducts lead direct to acini. This acinose type of gland gives great plasticity, so that the digestive mass can fill up all available space of the visceral mass (figs. 8 and 11, *d.gl.*, *d.gl.con.*, *d.gl.ant.*, *d.gl.d.*). The colour varies



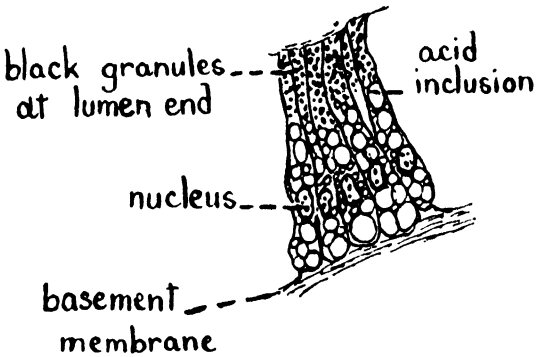
TEXT-FIG. 17. (*a*) Epithelium of stomach-cæcum in T.S. ×1,000. (*b*) Teased stomach cæcum epithelium, after vital staining with neutral red. ×750.

with the seaweed eaten, from orange to various tones of brown and green, but the ducts are always nearly black like the stomach gutters. These distinct regions show marked differences in the cells.

(i) The cells of the ducts are elongated flask-shaped and are ciliated only near the digestive gland orifice. In their narrow necks they have black-brown pigment granules containing iron and their wider parts have metaplasmic inclusions, some of which stain intravitally with neutral red (Text-fig. 18). They show some resemblance to the cæcum cells and they are probably the most active cells in secreting digestive enzymes

diastase, lipase and protease capable of acting in acid media.

(ii) The cells at the crypts of the acini are about the same size as the duct cells, but have very indefinite outlines (Text-fig. 19). They are darkly coloured in fresh and preserved material, owing to accumulations of refractive green-brown granules. These are angular. Histo-chemical tests show that much iron is present in

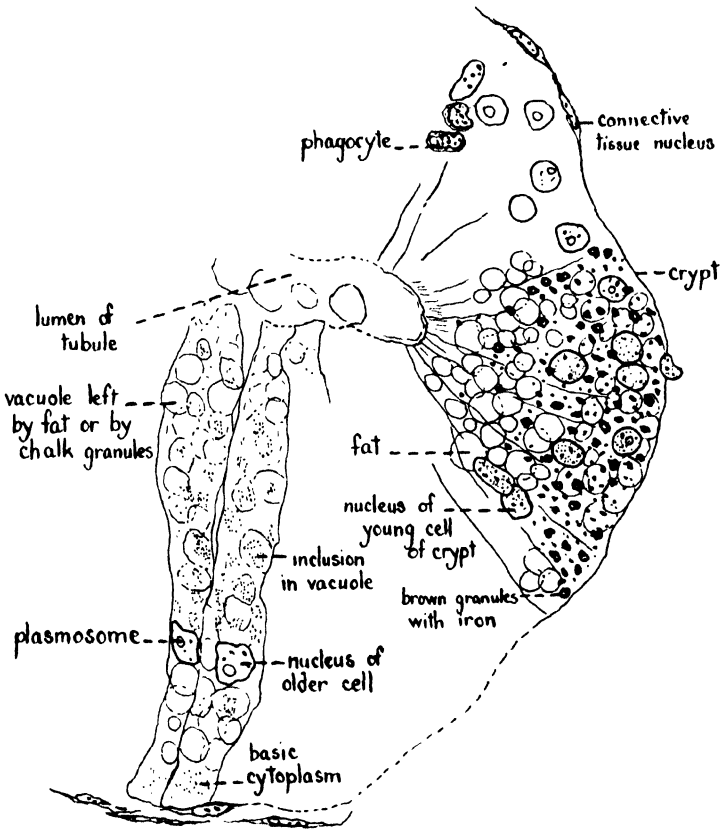


TEXT-FIG. 18. Duct cells of digestive gland. The large vacuoles are red after vital staining with neutral red. ×1,100.

them (Prussian Blue reaction and Macallum's test were used). In a fresh condition there are also masses of yellow refractive drops. In frozen sections, treated with Scarlet R., all the crypt gives intense fat reaction. In paraffin sections the cytoplasm stains deep violet, like pancreatic islets, with Methyl-green and pyronin of Unna. It is, therefore, strongly oxyphil and the cells are probably active like the duct cells in production of ferments.

Spherical nuclei are numerous and show division. From this fact, and from the indefinite and crushed cell outlines, it seems likely that these crypts are composed of young cells, such as Macmunn and, later, Yonge, in 1927, described in the digestive gland crypts of Lamellibranchs. Phagocytes are occasionally present in this part of the acini.

(iii) The older cells of the acini become larger and are more sharply distinguished from the crypt cells, the further they are removed from them (Text-fig. 19). They are very tall cylindrical cells with much cytoplasm and more defined outlines than the young cells. Their basal



TEXT-FIG. 19. Part of digestive gland tubule to show crypt cells and large cells. ×900.

nuclei are more irregular, stain weakly with nuclear stains, but have a distinct karyosome and plasmosomes. The pronounced difference is in the basophil cytoplasm and its inclusions. It has large fat vacuoles, but fat is less abundant than in the crypt cells and there is much

less iron. Chalk granules are scattered in the cells. They appear as large vacuoles in sections of acid fixed material, but in microscopic preparations of fresh cells they are seen to dissolve in weak acid. There are no separate chalk cells in *Haliotis* as in some Mollusca. Spherical granules and angular particles of varying size up to 6μ, which are greyish in sections with all stains, appear to be included in vacuoles. These suggest food vacuoles containing protein. The free cell surface sometimes has a distinct cuticle, but often this is lost and the cell surface is irregular. The cells vary according to their state of activity. These facts suggest the possibility of some intra-cellular digestion in the older parts of the acini. The colour of the digestive glands may be due to the ingestion of seaweed pigments, including iron associated with proteid. Indian ink added to the water in which small *Haliotis* are living is taken up in the digestive gland cells (cf. Yonge on Lamellibranchs, 1926).

PHYSIOLOGY OF THE STOMACH, ITS CÆCUM AND DIGESTIVE GLANDS.

The main function of the stomach is to collect the food, already mixed with secretion from the salivary gland and buccal pockets, to supply it with additional acid secretion from the stomach cæcum and with the secretion from the digestive glands. The stomach retains the mixture as long as possible, so that seaweed particles are digested. The gut contents are kept in motion by cilia; peristalsis can only occur in the narrow part of the œsophagus and to a less extent in the stomach, which alone have muscular walls. The alimentary canal is mainly thin walled. The digestive glands produce the copious enzyme-containing fluid perhaps mainly from the ducts and crypts, and probably aided by the cæcum. The yellowish granules of the secretory cells show some resemblance to zymogen granules and may be converted to enzymes. Large particles of weed are prevented from entering

the gland orifices by well-developed valves and these, covered with powerful cilia, control the direction of flow of the digestive fluid into the stomach gutters along the antero-ventral side near the crop opening. The gutters lead to the deep anterior gutter of the cæcum. It seems obvious that the digestive juice runs into the cæcum by the help of a powerful ciliary current produced by extremely long cilia on the ridges at its entrance. Therefore the cæcum acts as a collecting bladder; it is also a physiological extension of the stomach, collecting the fluid part of the food and mixing it with digestive enzymes by the movements of its cilia. It possibly also acts as an additional digestive gland. Its granules resemble zymogen granules.

The storing of digestive juice is probably the most important function of the cæcum of *Haliotis*, but in *Aplysia* all the food mixed with this fluid must pass up one side of the cæcum and down the other. (Mazzarelli and Zuccardi quoted by Eales.)

In *Haliotis* the stored fluid passes back to the stomach by the left, more posterior gutter. This gutter is kept separate, except at the blind tip, by a typhlosole. Absorption may commence in the migrating blood cells which penetrate through the epithelium of the crop, cæcum, liver and intestine, and find their way to the digesting food near the epithelium. Phagocytes are also seen ingesting bacteria. The older cells of the digestive glands may digest minute fragments by intra-cellular ferments.* It is possible that a different type of food is selected for absorption in the cæcum from that absorbed in the intestine. The latter shows great length, as in herbivorous animals generally.

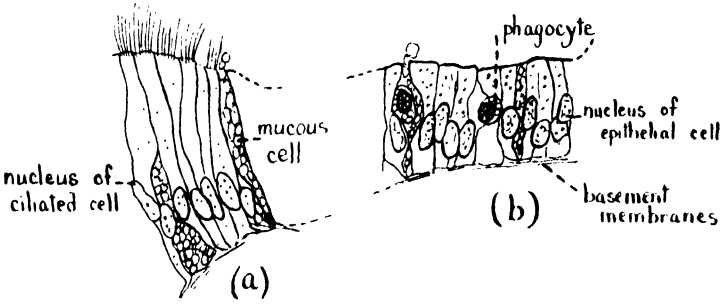
* In Lamellibranchia, particularly in the Order Septibranchia, the digestive gland cells assimilate proteids, but these animals are, of course, carnivorous. (Yonge, 1926-27).

IV. INTESTINE (fig. 8, and Pl. VIII, *T.S.*—C, F, G, H, K).

The intestine is long and provides a large surface for absorption of the digested seaweed. It meanders to fit in with the other viscera. The pyloric end of the stomach continues into the first part of the intestine, with only gradual narrowing of the canal. The separation of the two regions is marked by the presence of the pocket valve (V_3), with its edge pointing into the intestine, preventing regurgitation of food, and by the disappearance of the cuticular stomach lining. This first section of the intestine Vayssière labelled "third stomach." The ventral stomach gutter continues into the intestine along its right side. There are ridges each side of it and gutters outside these, so that there is a double typhlosole, extending longitudinally throughout the intestine, almost to the anus. The intestine lies beneath the pericardium, lying dorsal to the œsophagus. Its diameter is here much reduced, but it changes little from here to the anus. Beneath the posterior end of the respiratory chamber it bends suddenly to the right and passes dorsally over the right renal organ, then follows closely the left margin of the large shell muscle, where it is covered only by integument. Immediately anterior to the shell muscle it is bent back through almost 180° and the second limb of the intestinal loop is parallel to the first, lying between it and the œsophagus (figs. 8 and 10, and *T.S.*—F, *int.* 2). The intestine then re-crosses the œsophagus dorsally, passes ventral to the pericardium, turns again through 180° and enters the posterior end of the pericardium, where it traverses the ventricle, as in most Rhipidoglossa (figs. 8, 13, 30, 31 and 39). This part cannot be differentiated from the rest of the intestine, although it is sometimes termed the "rectum." It continues anteriorly in the roof of the respiratory chamber, covered by the mucous glands except in the last small section. This last section is swollen and is distinguished

internally by four to six longitudinal pleats of the epithelium. These allow for expansion of the lumen. There are the same number of projections at the anal opening, which is controlled by a small sphincter. The fæcal matter is discharged mainly through the shell perforations in the manner already described. (*Vide* Respiratory System.) The anus is usually on the right side in dextral forms, but in *Haliotis* the relatively enormous development of the shell muscle keeps it to the left.

The whole of the intestinal epithelium, with the exception of the longitudinal gutters, has ciliated and mucous cells (Text-fig. 20). The change from the stomach



TEXT-FIG. 20. (*a*) Ciliated intestinal epithelium. ×900.
(*b*) Epithelium of intestinal gutter. ×900.

epithelium is not sudden. Cilia are particularly long on the pleats near the gutters and near the anus. They help the forward movements of undigested fragments. Sometimes recognizable portions of weed, sand-grains, etc., are seen to leave the anus. The ciliated cells have granular contents. In the gutters the cells are much lower and resemble the glandular cells of the stomach gutters (Text-fig. 20).

Migratory blood cells are very frequently wedged between the epithelial cells, at various levels. These probably help in absorption of food and bacteria. Many mucous cells are present in the gutters and their secretion

probably lubricates. The heavier waste particles may drop into the gutters and get swept along in mucus by the very long cilia of the pleats. The contents of the intestine are distinctly less acid than those of all other parts of the gut.

The whole of the alimentary canal is richly supplied with blood. (See Blood Vascular System.)

Surrounding the whole of the digestive system there is a sheath of connective tissue. This is lymphoid and very extensive around parts of the digestive gland, stomach, and intestine (figs. 10, 11, 39, *l.t.*). There are large cells and blood cells in all stages of development. (See Lymphoid Tissues, p. 99.) This tissue has not hitherto been described ; it probably keeps up the supply of amœbocytes concerned in ingestion of bacteria and in absorption in the digestive canal.

CŒLOM.

It is well known that the cœlom in Mollusca is represented only by the pericardial cavity and the reduced gonadial and renal cavities. The cavity of the gonad is visible only in very young specimens of *Haliotis*; in older animals it is almost obliterated by the sex products. The renal cavities are extensive. The lacunar part of the blood vascular system develops into a hæmocoele at the expense of the cœlom, but in *Haliotis* it is unable to develop into a large space, because the great development of the right shell muscle and epipodium keeps the visceral mass compressed.

The pericardium can be seen in dorsal view immediately the shell is removed and its position is already described (fig. 12, *pe.c.*). The dorsal wall is transparent and the heart beats can be counted without removing it. The pericardial cavity provides adequate room for dilation of the three large heart chambers.

[Make an incision in the roof of the pericardium, avoiding injury to the auricles, which adhere to its anterior part, and to the walls of the renal organs. Examine the heart and lift the ventricle to see the left reno-pericardial opening.]

It is now seen that the pericardium has free walls only on the dorsal and left sides. Its whole antero-ventral cœlomic epithelium is grown on to the wall of the left renal organ (papillated sac) and mucous glands ; the left, the posterior, and part of the ventral walls adhere closely to the wall of the right renal organ (figs. 12, 29, 30, 31).

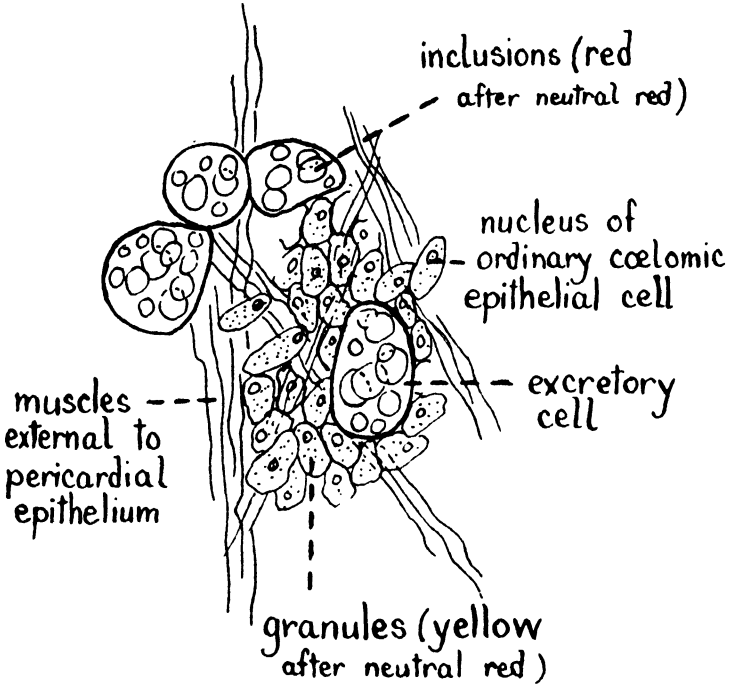
The cœlomic epithelium is covered by an extremely thin layer of connective tissue, with delicate blood channels, and the free surfaces have delicate interlacing muscle fibres and nerves beneath the thin integument. The nerves are described with the nervous system. Internally, particularly on the lateral walls, there are scattered large cells which have not previously been described in *Haliotis*. These are oval and have numerous large cytoplasmic inclusions, which stain very vividly with neutral red and Janus-green (intra-vitam), in contrast with the small non-staining inclusions of the small cœlomic epithelial cells surrounding them (Text-fig. 21).

They appear to be excretory cells, which discharge their granules and frequently the whole cell into the pericardial fluid. The auricles also excrete a watery fluid, which becomes part of the pericardial liquid. This colourless secretion, with disintegrating cells, contains uric acid. It passes through the left reno-pericardial canal into the cavity of the left renal organ, probably aided by heart pulsation and ciliary movement at the renal end of the canal. From here it escapes with the viscid secretion of the renal organ, through its opening in the posterior roof of the respiratory cavity. This final expulsion may be assisted by the dilation of the left auricle, which appears to cause a violent anterior push on the wall of the left renal organ.

After dissection and injection of numbers of specimens

of all ages, both fresh and preserved, and, after studying transverse, horizontal, and vertical longitudinal sections of very tiny and older specimens, I have been unable to find an open right reno-pericardial canal, although the left one is very obvious.

In spawning specimens I never found genital products in the pericardial fluid removed carefully with a syringe.



TEXT-FIG. 21. Excretory cells of pericardial wall. ×1,000.

Living animals were used as a last test. Catheters were fixed in the right and left external renal openings, after the mantle cavity had been opened, and a small quantity of sea-water coloured with carmine was injected with a hypodermic syringe into the pericardium. The red colour appeared in the catheter of the left renal organ only, each of the six times the experiment was repeated.

The left reno-pericardial orifice, lying in the floor of the pericardium, is readily seen if the ventricle be pushed on one side (fig. 13, *l.ren.p.c.*). It shows well in horizontal sections (fig. 31).

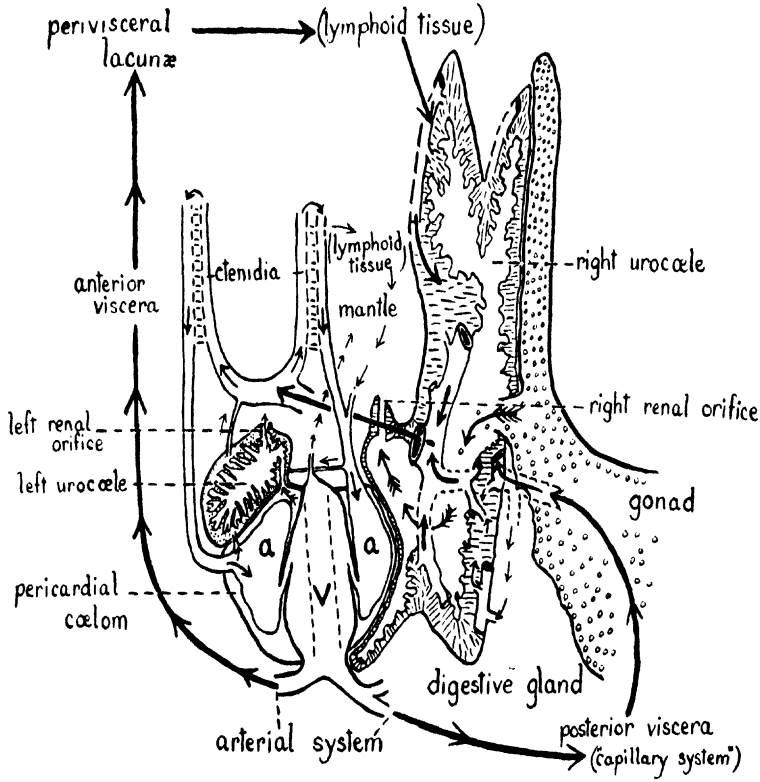
CIRCULATORY SYSTEM.

(Figs. 12 to 17, 29 to 31, 35 to 39, and Text-figs. 15, 22, 24.)

To provide adequate oxygenation for the powerful muscular movements of *Haliotis*, both respiratory and circulatory systems are well developed, although they show primitive features. The ctenidia are described under Respiratory System. The blood vascular system shows features of special interest. The heart demonstrates excellently those archaic characters of the organ which are found in most members of the Rhipidoglossa. The auricles are posterior to the ctenidia and are symmetrically placed on each side of the ventricle, which surrounds the intestine as in Lamellibranchs.

Text-fig. 22 shows the scheme of circulation. With the small exception of blood from the rectum, all the deoxygenated blood passes through the portal system of the right renal organ, before going to the ctenidia for oxygenation. Therefore all the blood passing through the ctenidia has excretory products already removed. This is another archaic feature. The oxygenated blood is conveyed from the ctenidia and mantle, which is the accessory respiratory organ, by the efferent ctenidial vessels, each of which receives a mantle vein and enlarges posteriorly to become the corresponding auricle (figs. 12 and 14). The heart, therefore, contains oxygenated blood. The presence of a small pallial artery at the anterior end of the ventricle, in addition to the posterior arterial trunk, gives a superficial resemblance to the heart of dibranchiate Cephalopods and to that of

Lamellibranchs. Wegmann emphasises the latter similarity. The large posterior trunk gives off the abdominal arteries directly after leaving the heart and continues as the anterior aorta ; it is therefore homologous with the anterior arterial trunk of Opisthobranchiata.



TEXT-FIG. 22. Scheme of circulation and arrangement of cœlomic cavities.

The anterior aorta carries blood to all the viscera anterior to the heart. It then passes to the peri-visceral lacunæ and, after passing through the lymphoid tissue surrounding the right renal organ, it empties to the afferent renal vessels by pores in their walls. The abdominal arteries

break up into a " capillary system " over the posterior viscera and a venous system collects the blood also to the afferent renal veins, which break up to renal lacunæ. The efferent renal veins carry the altered blood to the basi-branchial sinus, from which it passes to the ctenidia.

The anterior aorta partly surrounds the basal part of the radular cæcum, but it finally becomes the cephalic arterial sinus, which envelops the radular sheath. It opens with surprising suddenness into a special portion of the cephalic hæmocoele (Text-fig. 15). The first part of this is an arterial sinus, separated by definite muscular and connective tissue partitions from the venous cephalic lacunæ (figs. 35 and 36). The priority of this discovery in *Haliotis* and *Patella* belongs to Milne Edwards. More recent works assume that this cephalic sinus is not a distinct arterial portion of the hæmocoele, but I emphasise the truth of Milne Edwards' early observation, although I do not agree with him and all other observers that the sinus completely surrounds the radular cæcum. As in Gastropods generally, sinuses take the place of a capillary system in most parts of the body. The sinuses and lacunæ have no true endothelial walls but, whenever the direction of movement of blood is well defined, as in the arteries, in the venous sinuses connected with the right renal organ and the digestive system generally, the surrounding connective tissues and muscles are arranged parallel with the length of the blood canals, which are therefore physiological vessels and capillaries. The development of these walls is possibly stimulated by the blood flow.

The circulation of the left renal organ (papillated sac) differs remarkably from that of the right renal organ. Its connection with the bases of both efferent ctenidial vessels is difficult to explain (Text-fig. 22). The details are given under Auricles and under left Renal Organ.

THE HEART.

Haliotis shares with *Fissurella* and *Pleurotomaria* the bilateral symmetry of the two auricles, but unlike these genera, *Haliotis* has the pericardium displaced to the left. All three heart chambers are posterior to the ctenidia, as in all Aspidobranchs. The ventricle is slightly oblique, the posterior end lying more to the left than the anterior end (fig. 12). The heart beat can be watched through the transparent pericardial wall. The pulsations vary from 27 to 36 per minute, but the variations do not appear to bear any relation to the size of the animal.

1. **The Auricles** are merely swollen terminations of the efferent ctenidial vessels. The right auricle is a little larger than the left, which is often pushed ventrally; it receives oxygenated blood from the smaller of the two ctenidia, but more blood from the mantle than does the left auricle (fig. 12, *pal.v.r.*). Together the auricles hide most of the ventricle. The walls are diaphanous, with very delicate lace-like strands of muscle and fibrous tissue. Both auricles adhere slightly to the pericardial wall at their anterior ends (fig. 13). At the junction of the efferent vessel and the auricle there is a right opening and a left semi-circle of tiny apertures, variable in number. In *Haliotis tuberculata* the openings are (fig. 13):—

1 (*eff.a.*) The aperture from the right pallial vein, lying much anterior to the other openings.

2 (*eff.b.*) An aperture on the right side, belonging to a small pericardial vessel.

3 (*eff.c.*) An opening in the left semi-circle connected with a vessel in the ventral parts of the much-modified left renal organ, passing on its way over the orifice of the right renal organ.

4 (*eff.d.*) An opening, also in the left semi-circle, connected with a vessel of the left renal organ on its dorsal and ventral walls. Often there are two of these.

The apertures connected with vessels of the left renal organ are usually in a depression guarded by a valve, which would allow passage of blood from the right efferent ctenidial vessel to the vessels of the left renal organ. A row of very minute flaps are a little posterior to the valve and guard the entrance to the auricle (fig. 13).

There are similar openings at the junction of the left ctenidial vessel in the posterior wall of the left renal organ. These anastomose in the renal tissues with those from the right efferent ctenidial vessel.

When a minute quantity of coloured fluid is injected into the efferent vessel in living specimens it invariably passes direct to the vessels of the left renal organ, and only after the injection fluid has filled these tiny vessels, or during violent injection, does it pass into the auricles. The experiment was repeated many times and on one occasion a minute bubble got in with the speck of injection and this showed alternate movements, lasting two hours, to the left renal vessels at systole and out again to the top of the auricle at diastole. It is possible that these vessels are filled and emptied in this way ; heart pulsation causes obvious movements in the posterior wall of the left renal organ and may help circulation in its vessels, for diastole of the left auricle would push up the renal wall and force blood back to the base of the efferent ctenidial vessel.

This experimental evidence agrees in the main with the theoretical ideas of Fleure and Perrier regarding the circulation of this renal organ in *Haliotis* and *Patella*. The pericardial wall appears to be supplied with blood in a similar way.

Cytology and Physiology of Auricular Appendages (Pericardial Gland of Grobben).

The auricular appendages are dense fringes derived from simple diverticula of the auricle wall. They are better developed in *Haliotis* than in any other member of the

Aspidobranchia. They occur along that border of the auricles which is flattened against the ventricle, as various writers have observed, but there is also a line of fringes passing at right angles from the tip of the auricle part way along the external wall (figs. 13 and 15 *aur.ap.*). These minute sacculations pulsate with the auricle. Their walls are composed of the cœlomic pavement epithelium of the pericardial cavity. The cells are generally exceedingly flattened, so that the straw-coloured nuclei with yellow-green nucleoli hump the cells. The cytoplasm is colourless, transparent, and without granules. It is difficult to stain. The cells are separated from the auricular cavity by anastomosing and ramifying delicate muscular strands (figs. 13 and 15). These and the epithelial cells are directly bathed with blood, because the heart chambers have no endothelium. Closely packed blood cells drop into the sacculations and are intimately associated with the epithelial cells. Delicate pseudopodia of the blood cells are caught up in the muscular meshes of the fringes. In the living conditions amœboid movement of these blood cells can be seen; effete corpuscles are very occasionally found in the pericardial fluid outside the auricle wall, suggesting migration through the walls although such movement has not been witnessed. When the fringes are stained intravitally granules in the blood cells stain red with neutral red and there are blue vacuoles of trypan blue, but the epithelial cells do not stain. When the sacculations contract with the auricle the blood cells are seen to be squeezed when portions are watched microscopically and it is possible to concur with Grobben that fluid then passes from the blood cells through the flattened epithelial cells, which may function in straining off fluid excretion like the cells of Bowman's capsules. It is impossible to agree with Grobben that the cells are of glandular type, but nevertheless they may be a distinct part of the diffuse excretory cells of the pericardial wall, differing markedly

in their shape and contents from those on the lateral and ventral walls. (*Vide* Pericardium.)

Cuénot states that Wegmann is wrong in suggesting that fresh amœbocytes are manufactured in the auricle fringes, but this possibly does occur, as in the heart wall, etc., in higher Gastropods. Blood cells in the fringes are sometimes in the process of division. Possibly, therefore, the auricular appendages function as a lymph gland as well as an accessory part of the excretory system. In sections of specimens only 2 to 4 mm. long the fringes are not present.

The auriculo-ventricular openings are near the centre of the internal auricle walls. These crescentic apertures open anteriorly to the ventricle.

2. **The Ventricle** has thick opaque muscular walls. When cut open, as in fig. 13, the posterior two-thirds of its cavity has a spongy character, because muscular strands suspend the ventricle wall to the wall of the intestine, which passes through the ventricular cavity from end to end. Some of these short attachments must be cut to see the details of the ventricle. Anteriorly there are longitudinal bands of muscle inside the outer wall and in the posterior region the interlacing muscles suspending the intestine arise irregularly among the longitudinal muscles. To prevent regurgitation a three-fold valve points posteriorly into the ventricle and is held down by muscular bands resembling chordæ tendineæ (fig. 13, *aur.ven.v.*). As the section in fig. 31 shows, the cavity of the ventricle is a blood space between the muscles of the external ventricle wall and the incomplete endothelial internal wall overlying the circular muscles of the gut wall.

BLOOD VASCULAR SYSTEM.

[INJECTION. The vessels of the renal organs and digestive system can be seen without injection. Preserved specimens can be injected best after formalin-alcohol-

glycerine preservation, but the results are of course better with fresh specimens. After narcotising, the shell is removed as described on p. 29 and the animal is placed in 5 per cent. formalin in sea-water to get rid of the mucin.* Then Robin's cold gelatine injection mass (carmine) is injected into one of the efferent ctenidial vessels, into the median pallial vessel or directly into the ventricle. The best results were obtained by slow injection. The specimens are then hardened in 5 per cent. formalin in sea-water. The venous system can be injected in blue from the circular mantle vein or into the lacunæ of any part of the body. If small specimens are injected they are most useful when cut into transverse sections, by hand, after paraffin embedding. To trace specially difficult details, a little solid coloured gelatine can be passed into vessels by a bristle and pushed to pass into the fine ramifications. (Lacaze-Duthiers and Wegmann.)

DISSECTION. Trace the vessels of the mantle (see Venous System). Lift up the integument and gonad sheet from the digestive glands (see instructions before Digestive System and fig. 17), cutting the minute blood channels holding the gonad to the liver. Follow the dorsal circulation of the digestive gland and other viscera shown in fig. 17. Remove the pericardium to expose the origin of the arterial trunks. Cut through the dorsal roof of the anterior part of the right renal organ, as shown in fig. 17. Next cut through the muscles attaching the ventral side of the flattened visceral mass to the ventral mantle-plate. If other animals are available, remove a large portion of the posterior and left parts of the muscle as shown in fig. 14, and continue dissection from the ventral side. If the specimen is required for dissection of the pedal nerve cords, the visceral mass can be severed from the posterior end of the shell muscle and the whole mass rolled over.]

1. ARTERIES.

In contrast with the bilaterally symmetrical heart, the arterial system is very asymmetrical, with the exception of the pedal and epipodial arteries and the cephalic circulation. (Unless otherwise stated the vessels are unpaired.) The arteries which arise from opposite ends

* Dakin's Injection Method, "Liverpool Marine Biol. Com.," Vol. XVII, 1909, p. 76, and Mozejko's method of occluding vessels impossible to ligature with cotton-wool soaked with gelatine and plaster of Paris, are useful.

of the ventricle are the median pallial artery, from the anterior end, supplying the mantle, and the aortic trunk, from the posterior end, which supplies the remainder of the body.

The Median Pallial Artery (fig. 12, *pal.a.m.*) is a small artery arising from the extreme superior end of the ventricle. Shortly after leaving the pericardium, it arrives on the dorsal surface between the two halves of the mucous gland. There are fine parallel branches supplying the mucous gland lamellæ and, near the base of the mantle cleft, it forks to supply both sides of the mantle and its tentacles bordering the cleft. Shortly after leaving the ventricle, there is a small rectal branch (fig. 14, *rect.a.*). Fleure states that this pallial vessel is an erratic one, hardly worth calling an artery, but it is always clearly defined and it is easy to inject the whole arterial system from it. It is a peculiarity shared with *Fissurella*.

The Common Aortic Trunk is the main arterial trunk typical of Gastropods. In *Haliotis* it leaves the posterior end of the ventricle (fig. 14, *ao.tr.*). When it is slit open a large ventral semi-circular valve is seen. This prevents regurgitation of blood to the ventricle. The common trunk gives off two posterior abdominal arteries and two secondary arteries, then continues as the anterior aorta, supplying the anterior regions, foot and shell muscles. The arteries are described in order of proximity to the ventricle.

1. **Reno-intestinal Artery** (fig. 17, *ren.int.a.*). This short artery leaves the common trunk immediately after its origin from the ventricle and can be seen on the left side of the base of the ventricle. Usually it branches at once to supply the part of the intestine underlying the pericardium and the right renal organ. This small artery has not been described previously. The right renal organ receives mainly de-oxygenated blood from the afferent renal veins.

2. **First Visceral Artery** (fig. 14, *visc. a.* 1). This leaves the posterior ventral side of the common trunk at right-angles and supplies all the posterior parts of the visceral mass. It passes to the outer left side of the crop. Its two main branches are dorsal and ventral:—

(*a*) *The Ventral First Visceral Branch* continues the direction of the main artery and supplies the ventral parts of the liver, stomach and cæcum, disappearing in the reduced visceral spire (fig. 14, *visc.a.* 1. *v.*).

(*b*) *The Dorsal First Visceral Branch* passes up to the dorsal surface, where it is clearly seen through the integument (figs. 12, 14 and 17, *visc.a.* 1. *d.*). It skirts between the stomach, digestive gland and gonad and supplies numerous branches to all three. One branch goes to the constriction between stomach and crop. Fine branches ramify over the dorsal surfaces of the cæcum near the visceral spire.

3. **Intestinal Artery** (fig. 14, *int.a.*) is a small artery arising from the anterior side of the common arterial trunk and supplying the commencement of the intestine.

4. **Second Visceral Artery** (fig. 14, *visc.a.* 2) continues the direction of the common aortic trunk, passing obliquely under the crop and resting on the strip of digestive gland between the crop and the intestine. It is larger than the first visceral aorta and skirts the right shell muscle to the tip of the conical visceral appendage. Dorsal and ventral branches supply the gonad, digestive gland, crop and the ventral visceral integument. This has been called the genital artery, but the first visceral artery also takes part in supplying the gonad.

(*a*) *Hepato-genital Arteries* (figs. 14 and 17, *gen.hep.a.*). They extend on the dorsal and ventral surfaces of the visceral mass, mainly on its conical appendage, and lie between the digestive gland and the ensheathing gonad. The two largest of these arteries arise close to the shell muscle.

(*b*) *Tegumentary Artery* (fig. 14, *teg.a.*). This arises near the posterior end of the right shell muscle and passes to the continuation of the ventral mantle-plate into the visceral integument.

(*c*) *Œsophageal Arteries* (fig. 14, *œs.a.* and *cr.a.*). These vary from three to five branches. Two to four of them arise near the proximal end of the second visceral aorta and supply the dorsal surfaces of the crop and œsophagus. A more distal branch passes out opposite the tegumentary artery, also going to the dorsal surface of the crop.

5. **Anterior Aorta** (fig. 14, *ant.ao.*). This large trunk curves round and passes anteriorly at right-angles with the common arterial trunk. Instead of narrowing along its course in usual arterial fashion, its diameter increases slightly as it becomes the cephalic aorta and then it suddenly opens into the wide cephalic arterial sinus surrounding the odontophore. Therefore oxygenated blood can reach the head regions directly and rapidly. There are strong circular muscles in its wall, produced by local arrangement of the musculature and connective tissues. The proximal portion of the anterior aorta can be seen through the ventral integument, lying parallel with the left efferent ctenidial sinus; soon it becomes hidden between the intestine and the œsophagus. The anterior aorta does not completely surround the radular sheath throughout its length as all previous authors have stated, but only the anterior part of it. The anterior aorta twists round the dorsal surface of the crop, but in the narrow œsophageal region it passes round the right side to become attached to the lateral part of the radular sheath, although more anteriorly it is on the ventral parts of this covering; finally it becomes the cephalic arterial sinus which completely envelops the odontophore (Pl. VIII, various transverse sections). Actually it is in the pretorsional ventral part of the radular sheath, but has taken part in the torsion of the alimentary canal. There appears to be no previous mention of this.

Along the course of the anterior aorta there are branches supplying the œsophagus, intestine, shell muscle, foot and epipodium :—

(*a*) *Œsophageal Arteries* (fig. 14, *œs.a.*) are variable in number, but there are two main ones supplying the dorsal wall of the commencement of the crop.

(*b*) *Intestinal Arteries* (fig. 14, *int.a.*) also vary in number. One or two branches, arising from the radular region of the aorta, are reno-intestinal, supplying the anterior tips of the right renal organ and the second limb of the intestinal loop (fig. 17, *ren.int.a.*). Therefore both posterior and anterior regions of the right renal organ have arterial supply, which has not been described before.

(*c*) *Œsophageal Pouch Arteries* are very short (fig. 14, *œs.p.a.*).

(*d*) *The Shell Muscle Artery* arises in the position shown in fig. 14, *sh.m.a.*

Cephalic Arterial Sinus (figs. 9, 14, 17 and Text-fig. 15). The cephalic aorta suddenly widens after a contractile orifice into the cephalic arterial sinus, which is separated by definite local arrangements of the connective tissue and muscular partitions from the venous lacunar spaces of this region. After making numerous careful injections, dissections and sections of injected specimens, it is not possible to agree with Fleure that Wegmann and Milne Edwards went too far in distinguishing this arterial sinus. It is, however, necessary to depart from all previous authors in their statement that the sinus encloses the pleuro-pedal nerve mass. It lies completely anterior to this mass (figs. 14, *T.S.*—C and F, Pl. VIII and Text-fig. 15) which lies behind its posterior wall and is surrounded by the venous lacunæ. In fig. 36 (*T.S.*—F) the cephalic aorta is still a distinct vessel, but the venous sinus is clearly separated from it at the side of the shell muscle (figs. 14, 35 and 36). The sinus passes ventrally to the odontophore musculature and passes dorsally

only as far forwards as the transverse line where the floor of the buccal cavity evaginates to make the radular cæcum. The ventral part of the sinus gives rise to epipodial and pedal arteries, with complete walls. When injection is very slow it fills these and also all the ventral lacunæ between the buccal musculature. More violent injection fills the cephalic venous sinuses.

The cephalic arterial sinus surrounds the ventral muscles of the odontophore, so that freshly oxygenated blood bathes them (Text-fig. 15). In living animals the backward and forward movements of the odontophore probably help blood-flow in the cephalic sinus, as Fleure has suggested.

(*a*) *Pedal and Epipodial Arteries* (fig. 14, Text-fig. 15, and *T.S.*—C, F, G). A posterior ventral dilatation of the sinus lies in a foot depression, anterior to the shell muscle. Its opening is controlled by a valve-like flap of the foot and body-wall muscles as seen in *T.S.*—C, *v*. From the dilatation arise :—

(i) Posterior Pedal Arteries (fig. 14, *ped.a.i.*). These are paired central vessels running parallel and lodged in the groove of the pedal nerve cords. They reach nearly to the extremity of the foot, where they become very small. Branches pass into various parts of the central muscular mass.

(ii) External Pedal and Epipodial Arteries (fig. 14, *ped.ep.a.*). This pair curve in the muscle near the origin of the epipodium. Branches supply most of the external parts of the foot and epipodium.

(iii) Anterior Pedal and Epipodial Arteries (fig. 14, *ped.ep.a.a.*). These are paired arteries supplying the most anterior parts of the foot and epipodium. They can be traced when the pedal nerve cords are dissected, but are best seen in transverse section.

During creeping movements turgidity can be produced by sudden filling of the network of venous and arterial

sinuses in the foot. The flow of arterial blood is controlled by the valve at the exit of the pedal and epipodial arteries. When the muscles of the foot and epipodium contract this valve is closed, and a similar arrangement for the venous pedal sinuses can prevent the blood leaving the foot (*T.S.*—F).

(*b*) *Ophthalmic and Tentacular Arteries* (fig. 14, *opt.a.*). A pair of arteries leave the cephalic arterial sinus at its widest anterior part. They soon branch into ophthalmic and tentacular arteries.

(*c*) *Anterior Buccal Arteries* (fig. 14, *buc.a.a.*). Arising from the sinus near the mid-ventral region of the buccal orifice, this pair of vessels surround the snout, supplying branches to the buccal papillæ. These have not been previously described.

2. Lacunæ and Venous Sinuses.

The lacunar system is formed by irregular hæmocœle spaces in the connective tissue in all parts of the body. This system serves for communication between the terminations of the arterial system and the venous sinuses. The spaces are most obvious in the mantle and in the spongy tissue surrounding the viscera. They allow for turgescence of the tegumentary organs to help in their movements, and bathe all the tissues with blood. In the cephalic region these lacunæ communicate by pores with the arterial cephalic sinus and they surround the salivary glands, œsophageal pouches and the nervous system. In the visceral regions the hæmocœle consists of small erratic perivisceral spaces. All these lacunæ show best in transverse sections. From the cephalic lacunar system the blood is collected into the cephalo-pedal sinus (Pl. VIII, *T.S.*—F, *ceph.ped.v.s.*). Ultimately this de-oxygenated blood and that from the abdominal lacunæ is discharged into the afferent veins of the right renal organ. The renal vessels constitute a renal portal system, for they discharge the blood to the basi-branchial sinus on its way to the afferent

ctenidial vessels. From the mantle lacunæ, blood discharges into the anterior abdominal lacuna (fig. 17, *pal.v.o.*), although a smaller part of the blood oxygenated in the mantle goes direct to the auricle, without passing through the right renal organ and the ctenidia. Therefore nearly all the de-oxygenated blood is altered in the renal portal system before going to be oxygenated (Text-fig. 22).

The venous sinuses have no true endothelium, but the neighbouring muscles and connective tissues arrange themselves to make muscular walls to propel the blood. In the right renal organ and on the surface of the digestive glands blood channels branch very definitely and resemble veins.

(*A*) **Cephalo-pedal Venous Sinus** (*T.S.*, F, *ceph.ped.v.s.*). This is posterior to the cephalic arterial sinus and lies against the hypertrophied shell muscle, which, together with the pedal muscle, makes part of its wall. A muscular sheet, which passes up from the central part of the foot, also makes part of the dorsal wall. The left wall is formed by a muscular band, which passes dorsally from the visceral surface of the foot. These muscles grow out as a valve which must press against the large shell muscle, when the latter is in a state of tonus, so that blood is prevented from emptying from the foot (fig. 36). This venous sinus has three main factors and one less important, discharging into it, in addition to the cephalic lacunæ.

1. *The Posterior Pedal Sinus* (figs. 14 and 36, *ped.s.p.*) is a large median sinus lying between the pedal nerve cords and running from almost the posterior extremity of the foot to the anterior end of the hypertrophied shell muscle. It receives factors from smaller sinuses and lacunæ ramifying throughout the main part of the foot and epipodial muscles. Two sinuses run parallel with it. They surround the inner sides of the pedal nerve strands and have transverse anastomoses.

2. *The Anterior Pedal Sinus* (fig. 14, *ped.s.a.*) carries blood from the anterior parts of the foot and epipodium and passes ventrally to the cephalic arterial sinus. The pleuro-pedal mass and the pedal nerves lie between the arterial and venous sinuses.

3. *The Shell Muscle Sinus* (fig. 14, *sh.m.s.*) leaves the central part of the right shell muscle to join the cephalo-pedal sinus.

4. *The Œsophageal Sinus.* A smaller sinus discharges from the walls of the œsophageal pockets. It is shown diagrammatically in fig. 14, *œs.s.* The abdominal lacunæ also receive blood from the œsophageal pouches. The cephalo-pedal venous sinus empties into the abdominal hæmocœle, beneath the anterior end of the intestinal loop.

(*B*) **Abdominal Venous System.** This system can be divided into anterior and posterior sections; both of these discharge to the renal portal system, which eventually leads the blood to the ctenidial vessels. It is therefore convenient to consider the abdominal venous system under four headings.

1. *Anterior Visceral Venous System.* Abdominal venous lacunæ pass in the connective tissue between the œsophageal pouches and the integument. The large circular pallial vein passes from the right mantle lobe attached to the hypertrophied shell muscle, under the conical appendage of the visceral hump, continuing near the edge of the ventral mantle-plate until it reaches the base of the left anterior mantle lobe, from which it receives a factor. It then empties to the left abdominal lacuna, just below the base of the left osphradium (fig. 17, *pal.v.*, *pal.v.l*, *pal.v.o.*). The abdominal lacunæ open by numerous little pores into thin sheets of lymphoid tissue surrounding the right renal organ and pass through it to the afferent renal portal veins, carrying some blood from the lymphoid tissue. A row of little openings from the abdominal lacunæ is clearly seen on the left side of the anterior

lobes of the right renal organ (fig. 29, *abd.l.o.*, and Text-fig. 22).

2. *Posterior Visceral Venous System.* The veins, which collect blood from the organs of the visceral hump and its conical appendage, make a delicate branching system mainly on the dorsal surface. They are readily seen when the gonad is lifted up with the integument (fig. 17). Some of these veins run parallel with the arteries. There are two main vessels :—

(*a*) *The Median Visceral Vein* runs diagonally, collecting blood from the reduced visceral spire, stomach and stomach cæcum, crop and parts of the digestive gland and gonad.

(*b*) *The Hepato-genital Vein* of the conical appendage runs parallel with the artery here and collects blood from the " liver " and gonad.

3. *Renal Portal System.* This system is intercalated in the flow of almost all the de-oxygenated blood to the ctenidia. One or sometimes two very small veins, bringing blood from the terminal part of the intestine direct to the basi-branchial sinus, are the only exception (fig. 17, *rect.v.*). The two posterior visceral veins carry blood to the anterior and posterior afferent renal veins (fig. 17, *aff.r.v.*), which have ramifying branches all over the dorsal and external surfaces of the right renal organ. They also receive branches from the neighbouring parts, mainly the digestive gland and gonad. The anterior afferent renal vein also receives the blood from the anterior venous lacunæ, as described above.

When the dorsal wall of the renal organ is cut open to the left of the afferent renal vein, its branches are cut as shown in fig. 17. The intricate lobes of the right renal organ, which are buried beneath the other viscera, are shown in fig. 29. The internal surface of the right renal organ has a honeycomb appearance and the surface is almost covered by a network of veins, the blood from which is collected by four main factors of the efferent

renal sinus (fig. 17, *eff.r.s.*). According to Perrier the very distended anterior factor conveys blood direct from the cephalic lacunæ, without alteration in the tissues of the right renal organ. This is incorrect. The wide efferent renal sinus curves up to run between the two external renal openings, immediately above which it becomes the transverse basi-branchial sinus. This receives the small rectal vessel and an equally small vessel from the very modified left renal organ (figs. 14 and 17, *l.ren.v.*). Wegmann states that the latter vessel is an afferent vessel of the left renal organ and that the peculiar vessels connecting the organ with the anterior end of the auricles are efferent renal vessels. (See "Auricles.") It seems unlikely that the blood in the minute renal vessel connecting with the basi-branchial sinus would have blood flowing in the opposite direction from the main stream of blood in the sinus towards the ctenidia. It is clear that the circulation of the left renal organ is entirely different from the renal portal system of the right organ. (See "Auricles" and Text-fig. 22.)

4. *Ctenidial Circulation.* The basi-branchial sinus passes blood to the left afferent ctenidial vein or to its counter-part on the right. The circulation in the ctenidial lamellæ and in the efferent ctenidial sinuses, carrying oxygenated blood to the auricles, has been described with the respiratory system.

Right Pallial Vein. This must be considered separately from the other mantle veins, for it conveys blood, which has been oxygenated in the mantle, directly to the heart. It is therefore another exception to the general scheme of blood passing through the right renal organ on its way to the ctenidia and finally back to the heart. The blood which it empties to the terminal part of the right efferent ctenidial sinus has, however, been oxygenated in the mantle (fig. 12, *pal.v.r.*).

BLOOD.

The blood is very faintly blue, owing to the presence of the oxygen carrier hæmocyanin dissolved in the plasma. Cuénot states that, in *Haliotis lamellosa*, the blood is more noticeably blue than in *Trochus* and *Fissurella*. Hæmoglobin is present only in the odontophore muscles of *Haliotis*, as in *Patella*, *Trochus*, *Aplysia*, *Limnæa*, etc., in which Lankester explains that it gives increased facility for oxygenation for these much worked muscles. The amœbocytes are almost colourless, although the inclusions, consisting of the various products of metabolism, may be faintly coloured.

The nucleus is usually spherical, although it may be polymorphic or even double. The living amœbocytes show very active amœboid movements, as can be seen from the camera lucida drawings in fig. 16. They measure from 5μ to 7μ in diameter, when the pseudopodia are retracted. In sections they are frequently circular in outline, but may show pseudopodia.

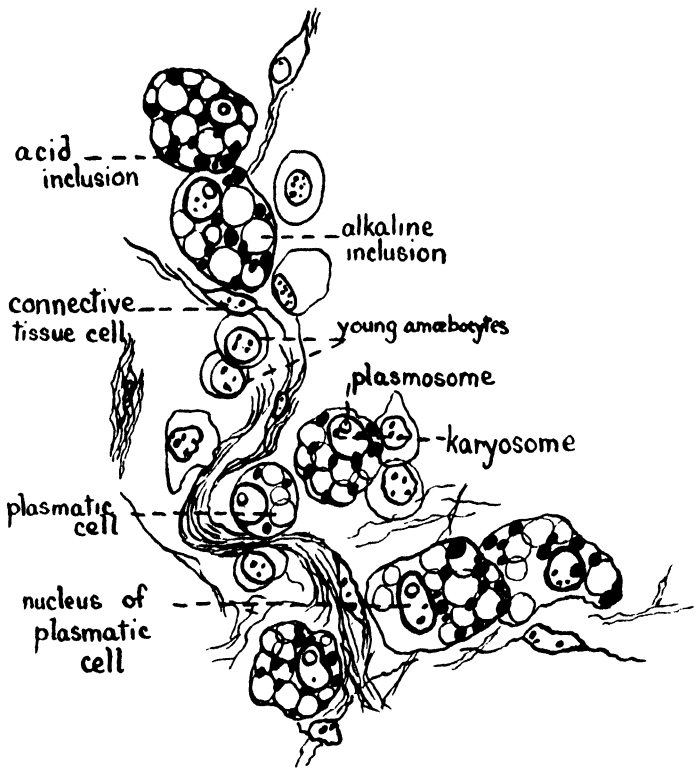
The volume of blood in the body is sufficiently large to produce turgescence of parts.

CONNECTIVE AND LYMPHOID TISSUE.

Connective Tissue is abundant between the viscera and between the muscle fibres of the mantle, particularly in the ctenidial supports. In all places it is fenestrated by the lacunæ of the blood vascular system and, with the muscles, it arranges to form walls of vessels. The connective tissue fibres are formed from cells each with a small oval or elongated nucleus and multiple cytoplasmic branches, which may be very elongated or star-shaped. They secrete a semi-gelatinous stroma. In addition to the amœbocytes caught in the meshes there are scattered very large cells varying from 15μ to 22μ in diameter. They are only abundant in the specialised lymphoid parts of the tissue.

When examined in the fresh condition they do not seem

to be amœboid, but have granules, which stain vividly with methylene blue and neutral red (intra-vitam) and huge alkaline inclusions (yellow with neutral red) which appear as vacuoles after acid fixation (Text-fig. 23).



TEXT-FIG. 23. Lymphoid tissue. ×1,000.

These are the "plasma cells" Leydig has described for Mollusca, and they are probably accumulative excretory cells. (Also see Excretory Organs.)

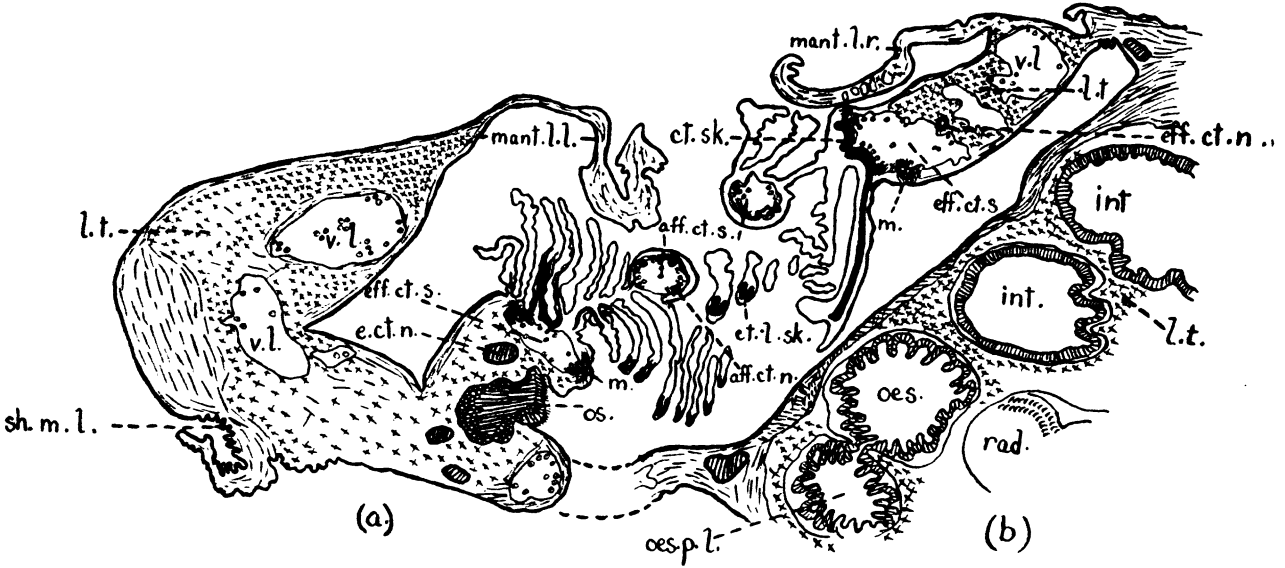
Lymphoid Tissue (Text-figs. 23 and 24). Lymphoid tissue is diffuse in *Haliotis*. In several regions this modified connective tissue is distributed in more or less irregular fashion and varies in amount in different individuals.

Cuénot, 1891, in his experimental work on the blood and lymphatic glands of Invertebrates, was the first to mention lymphatic glands in the supporting membrane of the ctenidia in *Haliotis*. I have been unable to find any reference to the patches of exactly similar tissue situated in the abdominal region, particularly near the right renal organ and surrounding all parts of the alimentary canal.

(*a*) *In the Ctenidial Supports.* In *Haliotis lamellosa* Cuénot described and figured poorly delimited lymphatic glands in the neighbourhood of the efferent ctenidial vessels. The branchial support of the smaller ctenidium on the right has its connective tissues sub-divided by irregular transverse septa and the intervening spaces are crammed with cells of the lymphoid gland, which is bordered on one side by the efferent ctenidial sinus and on the other by the mantle.

The larger ctenidium on the left has practically no mantle support and the lymphatic gland is here a small specialised part of the mantle next to the efferent vessel. Cuénot says there is undoubted evolution of blood cells in these glands. Dead amœbocytes are converted to a yellow ferment which is passed to the blood, and newly-formed amœbocytes have a very thin zone of protoplasm with refractive clear yellow granules ; when fully formed these are passed to the blood stream, since there is no definite membrane separating the efferent vessel from the gland.

In *Haliotis tuberculata* these glands are also present near the efferent vessels of the gills. Contrary to Cuénot's description for *H. lamellosa*, this tissue is not less abundant in the mantle connected with the larger ctenidium than in the branchial support of the right ctenidium. Serial sections show that on the left side it is very abundant in the thickened mantle immediately anterior to the mucous gland, but more posteriorly it gets less abundant



TEXT-FIG. 24. (*T.S.* E.) Position of lymphoid tissue in mantle. (*a*) Through left ctenidium at level marked in Fig. 17 (Plate IV). (*b*) Through right ctenidium at lower level shown in Fig. 17. ×14.

(Text-fig. 24 (*a*)). Conversely in the right ctenidial support there is little lymphoid tissue anteriorly, but about half-way down it is very abundant (Text-fig. 24 (*b*)).

In addition to the cells described by Cuénot there are numbers of the large plasmatic cells of Leydig, which are also scattered in the ordinary connective tissue.

The fine network which injects readily with the right and left pallial veins is the lacunar system of this lymphoid tissue. The blood probably passes through from the efferent ctenidial sinus to the gland, where it collects newly-formed blood cells and the products of destruction of old ones, and passes on to the mantle veins (Text-fig. 22). Wegmann clearly showed this vascular network, but he thought it drained the osphradia, which he erroneously considered as secondary ctenidia.

(*b*) *In the abdominal region* lymphoid tissue is in patches between all parts of the alimentary canal posterior to the buccal bulb and surrounds the right renal organ. It is thick around all parts of the intestine and between the right renal organ and the digestive gland. (See Transverse Sections, *l.t.*) When the intestine loop near the anterior end of the large shell muscle is lifted up, a nest of lymphoid tissue is seen, hiding part of the renal organ (figs. 17 and 29, *l.t.*). In the account of the circulation it was remarked that blood from the abdominal venous lacunæ passes by small orifices through this tissue to reach the anterior afferent renal vessel.

NERVOUS SYSTEM.

(Figs. 18 to 21, and *T.S.*, B, C, D, F, G.)

The nervous system of *Haliotis* is interesting because it is of the primitive streptoneurous type, with marked absence of concentration. The ganglia are elongated and flattened and a sheath of ganglion cells frequently spreads to the flat commissures and connectives. This archaic

feature, well shown in the elongated cerebral commissure, as in *Pleurotomaria*, is shared with the Polyplacophora. The pedal nerve centres are elongated into ganglionated cords, extending almost the whole length of the foot and with many transverse commissures. Such arrangement of the pedal cords is characteristic of the Aspidobranchia and recalls the ventral nerve chain of Annelids. Each pedal cord has a lateral groove, partly dividing it into dorsal and ventral moieties. This led to Lacaze-Duthiers' description of two distinct nerves in one " neurolemma " ; the dorsal one he called the " inferior pallial nerve " and, because it innervated the epipodium, he considered this structure to be a mantle formation. Apart from this error, his very detailed work is the foundation of our knowledge of the nervous system of *Haliotis*. His mistaken observation led to controversies between French authors, on the one side, and English and German authors, on the other. Spengel, 1881, correctly figured these strands as purely pedal centres, but Thiele, 1890, used Lacaze-Duthiers' error in his schematic figure of the nervous system of *Haliotis* to show an additional affinity with the Amphineura. The cerebro-pedal connectives join the dorsal section, as in *Fissurella* and *Incisura*. In *Haliotis* the pleural ganglia are no more differentiated than in *Pleurotomaria*, but they are fused to the dorsal surface of the anterior commissure of the pedal centres, so that no pleuro-pedal connective is present. There are long cerebro-pleural and cerebro-pedal connectives passing on each side of the odontophore up to the cerebral ganglia, which are very wide apart ("hypoathroid" arrangement). The optic and tentacular nerves join the cerebral ganglion separately, unlike those of *Pleurotomaria*. The cerebral ganglia have a large labial lobe which tapers to a fine labial commissure. This is present in the Amphineura and some Lamellibranchs, but only in the Aspidobranchia among Gastropods. The stomato-gastric

commissure originates from the first part of the labial commissure in primitive fashion. This buccal connective passes between the extrinsic and intrinsic odontophore muscles, and turns abruptly dorsalwards to swell into a pair of stomato-gastric ganglia between the radular cæcum and the commencement of the œsophagus. The visceral connectives, arising from the pleural region of the pleuro-pedal mass, show the usual streptoneuran twisting into a figure of eight, as a result of the torsion of the viscera, so that the pretorsional right connective is supra-œsophageal* and carried to the left, and the pretorsional left connective is infra-œsophageal and on the right side. These connectives are of the primitive lengthy type, with the ganglia wide apart. The lateral ganglia are equally developed on offshoots of the visceral connectives in the ctenidial supporting membrane and serve as branchial and osphradial centres. There is dialyneury on both sides, but on the right this anastomosis of the visceral connective with the pallial nerve of the pretorsional opposite side is long and passes close to the large shell muscle. This meandering connection has not been described before. The third ganglion of the visceral loop, the abdominal ganglion, is very diffuse. Its rectal nerve preserves primitive paired branches, but the visceral nerves, arising from the lateral extensions of the ganglion onto the visceral cords, are asymmetrical like the viscera they innervate.

[DISSECTION is facilitated by maceration in 5 per cent. potassium bichromate in sea water, or Béla Haller's mixture of one part glacial acetic, glycerine and two parts of water, from one day to a week. This shows up the opaque nerves against the translucent mass of pedal muscle. This difficult part of the dissection is also helped by using strong saline, which contracts the muscles away from the nerves. These show well, however, in hand transverse sections of various parts of the foot. (Specially

* Because of its great length the intestinal loop passes dorsal to the proximal part of the " supra-intestinal " visceral connective.

intricate details were elucidated with intra-vitam staining and Ranvier-Lœwit gold chloride method.)

The whole nervous system is enveloped in a connective tissue sheath enclosing a small lacuna, which is helpful for dissection.

Make a median dorsal incision through the body wall in the region of the head pleat to show the cerebral commissure. Continue the incision posteriorly, passing a little to the left of the anterior end of the large shell muscle. Open the pallial cavity by cutting along the mantle at the left and posterior borders of the hypobranchial glands. Turn the roof of the respiratory cavity over to the right. Carefully strip up the integument to see the superficial part of the supra-œsophageal visceral connective and remaining superficial parts of both visceral connectives with their branches (fig. 20). They can be located through the transparent integument before dissection. Remove part of the œsophageal pouches and lift up the intestinal loop to find the cerebro-pleural and cerebro-pedal connectives, pleuro-pedal ganglion mass immediately anterior to the shell muscle and the proximal part of the pleuro-visceral connectives. The left external pallial nerve is followed in the floor of the visceral mass but the right one must be followed through the anterior part of the large shell muscle.]

The nervous system is proportionately very large in minute specimens as shown in fig. 37.

(*A*) Cerebral Ganglia and Dorsal Commissure.

The cerebral ganglia are placed laterally at the anterior end of the buccal mass. They are widely separated by, though not sharply differentiated from, the stout transverse cerebral commissure. This lies immediately under the tegumentary fold between the cephalic tentacles. Sections show that it has superficial nerve cells, which are abundant in the dorsal surface near the ganglion, but medially there are few cells confined to the antero-ventral region. The cerebral ganglia and their commissure are flattened against the buccal musculature, so that their inner surfaces are concave. Posteriorly each ganglion has three divisions. Two lateral divisions become the parallel cerebro-pleural and cerebro-pedal connectives and

the ventral one is a tapering labial extension of the ganglion, which gives origin to the labial commissure and the cerebro-buccal connective.

Nerves arising from the Cerebral Ganglia.

The distribution of these sensory and tegumentary nerves is the same for right and left sides.

(*a*) *Tentacular Nerve* (figs. 18, 20 and 27, *t.n.*) arises from the posterior dorsal edge of the ganglion. It is easily confused with the smaller cephalic pleat nerve, which accompanies it, and with the snout nerves which arise from the ventral edge of the ganglion and commissure. The tentacle nerve is ganglionated as far as its entrance into the tentacle, in the centre of which it runs ventral to the tentacular artery. Branches supply the sensory structures of the tentacle (figs. 27 and 28).

(*b*) *Optic* (*Rhinophore*) *Nerve* (figs. 18, 20 and 24, *opt.n.*). Its origin is in the central part of the cerebral ganglion and, according to Fleure, optic fibres continue posteriorly to the origin of the cerebro-pleural connective. Branches arising along its whole course pass to the integument and muscles of the eye protuberance. Distally the nerve breaks up into fine branches with ganglionated anastomoses showing as a white network external to the black pigmented retina. Therefore the proximal part of the optic nerve is a collection of sensory and motor fibres.

(*c*) *Statocyst Nerve* (figs. 21 and 23, *stat.n.*, and Text-fig. 25). This is traced with difficulty. It passes round the origin of the visceral cord to the groove at the fusion of the pleural and pedal ganglia and then travels in intimate contact with the cerebro-pedal connective to the cerebral ganglion. This was first worked out by Lacaze-Duthiers.*

* Lacaze-Duthiers, after careful removal and arrangement of the œsophageal nerve ring, treated with oxalic acid, which makes a white oxalate with the calcareous statoliths. By tapping the cover-slip they are jogged through the thin lateral wall of the statocyst, travelling up between the fibres of the statocyst nerve ; further tappings send them gradually up the nerve.

It can be followed by intra-vitam staining with methylene blue and in serial sections.

(*d*) *Labial Nerves* (figs. 19 and 20, *lab.n.*). These nerves innervate the buccal orifice region. They are not constant in number. Each side, there are usually two dorsal labial nerves arising from the antero-ventral edge of the cerebral commissure close to the cerebral ganglion. Three more arise from the labial prolongation of the ganglion. Finally a thin labial nerve passes from the middle commissure region to the floor of the buccal opening, making six and sometimes eight labial nerves in all. They have no branches until they reach the sensitive lips.

(*e*) *Epipodial Nerve* (*ep.n.*1.). Arising slightly nearer the middle line than the tentacular nerve, the much thinner epipodial nerve originates almost on the cerebral commissure. It runs close to the tentacular nerve and is easily mistaken for a labial nerve, but it innervates the anterior terminal portion of the epipodium, which lies between the tentacle and the snout.

(*f*) *Cephalic Pleat Nerve* (fig. 20, *ceph.p.n.*). This small nerve arises externally to the optic nerve. It usually passes under the tentacular nerve and then goes dorsally to the pleat between the tentacles.

(*g*) *Tegumentary Nerves* of the head wall are usually two each side arising from the lateral region of the cephalic ganglion (*teg.n.*).

(*B*) Labial and Stomato-Gastric Commissures.

[Dissection. Cut round the anterior snout integument ventrad of the mouth slit and remove the whole snout wall on one side. Carefully sever the muscular and connective tissue attachments to roll up the odontophore. Follow the delicate labial commissure and the labial nerves not already dissected. The stomato-gastric connective can be seen passing between the musculature of the odontophore. Delicate dissection is needed to remove the muscles and expose the winding course of the connective with its branches to the roof of the buccal cavity

and into the salivary and buccal glands. Remove part of the roof and floor of the œsophagus immediately posterior to the opening of the radular cæcum to expose the stomato-gastric (buccal) ganglia with their commissure and nerves (figs. 19 and 20).]

Labial Commissure (*lab.co.*). The ventral portion of the cerebral ganglion tapers into the lateral part of the labial commissure, which slopes anteriorly to the very slender connection beneath the vertical mouth opening. Haller and others have denied the existence of this connection, which Lacaze-Duthiers saw, but sections and dissection show that it undoubtedly exists, although its thinness possibly indicates a tendency to loss of this primitive feature. The commissure has a sheath of nerve cells near the cerebral ganglion and in the median region, but it is scarcely possible to describe a foundation of labial ganglia as Thiele does.

Labial Commissure Nerves. These are similar for both sides.

(i) A short thin labial nerve innervates the mid-ventral region of the buccal orifice (*lab.n.*).

(ii) Three of the long labial nerves arise from the region where the cerebral ganglion merges into the labial commissure.

(iii) More laterally, a nerve has a branch to the ventral head wall and a winding branch ramifying to the ventral odontophore muscles and the tip of the radular elastic membrane (fig. 19, *od.n.*).

Buccal (Stomato-gastric) Commissure (*st.g.co.*).

The cord leading to the buccal (stomato-gastric) ganglion originates at the commencement of the labial commissure, so that it is very near the cerebral ganglion, from which it actually arises in the Pectinibranchia, in which the nervous system is more concentrated. In *Haliotis* the stomato-gastric cords have a course between the dorsal intrinsic and extrinsic musculature of the odontophore.

Flexions are necessary to allow sufficient length during protraction of the radular apparatus. The cords swell slightly into ill-defined buccal ganglia, lying between the radular sheath and the floor of the ventral valve region of the œsophagus (*buc.g.*). Between these ganglia is the short buccal commissure. Nerves arise from various parts of the lengthy stomato-gastric loop. They innervate the digestive tube.

1. *Nerves from the buccal commissure* (fig. 18, *rad.s.n.*) are an inner and an outer pair passing to the muscles of the radular sheath and to the radular membrane respectively.

2. *Buccal ganglion nerves* (fig. 20) are very fine; a posterior pair run into the ventral œsophageal valve, and an anterior pair go to the radular sheath and œsophageal pouches.

3. *Nerves of the buccal cords* are paired and arise from its lateral ganglionated region. The buccal ganglia are not sharply marked off from this region.

(*a*) Buccal nerve (fig. 20, *buc.n.*). This branches over the lateral and anterior dorsal region of the buccal cavity and anastomoses with its counterpart.

(*b*) Bucco-salivary nerve, originating somewhat more dorsally than the above, soon divides into two :—

(i) Buccal pocket and salivary gland nerve (*s.gl.n.*).

(ii) Bucco-œsophageal branch, innervating the posterior dorsal wall of the buccal cavity and with a special branch to the dorsal œsophageal valve (*buc.œs.n.*).

(*C*) Cerebro-Pleural and Cerebro-Pedal Connectives.

These form the lateral parts of the œsophageal ring. They lie beneath the head wall, passing round the buccal mass in the ventral region. There are few nerve cells in these connectives.

1. **The Cerebro-Pedal Connective** leaves the ventral posterior part of the cerebral ganglion and enters the ventral region of the pleuro-pedal mass (figs. 20 and 21).

Along its course two nerves arise, which pass obliquely in the head wall to penetrate the epipodium. They anastomose with each other and with the first epipodial nerve from the pedal cord (fig. 20).

2. **The Cerebro-Pleural Connective** leaves the lateral posterior part of the cerebral ganglion and enters the pleuro-pedal mass dorsal to the cerebro-pedal connective. It has a small branch to the head wall.

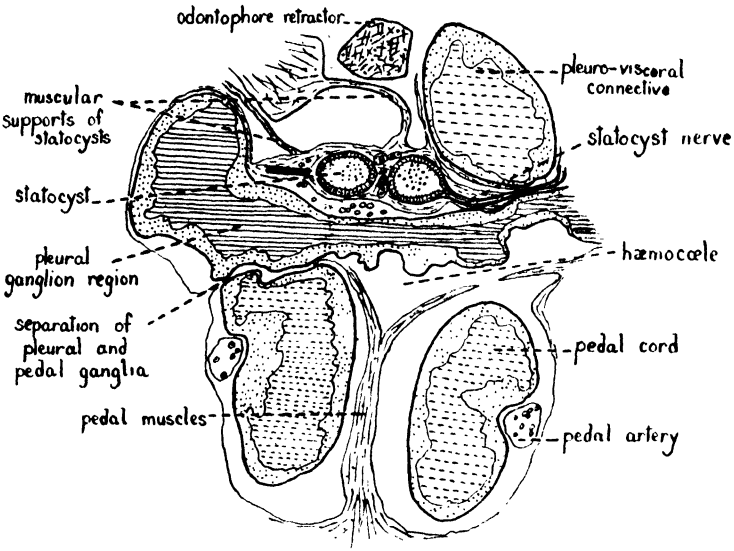
(*D*) Pleuro-Pedal Ganglion Mass.

This quadrilateral mass is lodged in a depression of the floor of the visceral cavity near the anterior border of the hypertrophied shell muscle, which must be removed before the prolongation of the pedal part of the mass can be followed into the foot muscle. It is impossible to consider the pleural and pedal ganglia apart, because the former adhere dorsally in an intimate fashion to the anterior end of the very elongated pedal ganglion cords. The pleural ganglia are only slightly differentiated by lateral grooves towards the posterior end of the mass. These grooves are dorsal to the lateral grooves in the elongated pedal cords and not continuous with them, as Lacaze-Duthiers supposed (Text-fig. 25).

The whole mass has a thick sheath of nerve cells, which spread a little distance on the four cerebral connectives, on the pair of pleural nerves and on the visceral cords. The nerve fibres are entirely internal and sections show that they are transverse between the pleural and pedal regions of each side (Text-fig. 25). These probably represent transverse commissures, possibly the dorsal anterior transverse fibres are pleural and the posterior ones are pedal.

The anterior pedal nerves arise from the most ventral part of the ganglion mass and the cerebro-pedal connectives merge into the dorsal part of the pedal region. The cerebro-pleural connectives and the pallial nerves

merge into the dorsal pleural moiety of the ganglion mass, but the stout visceral cords are most dorsal and are vertical to the surface of the ganglion mass.



TEXT-FIG. 25. T.S. through anterior end of pleuro-pedal ganglion mass. ×50.

Pedal Ganglion Cords (figs. 20 and 21, and *T.S.*—F and G, *ped.cd.*).

These stout ganglionated cords are a continuation of the ventral part of the pleuro-pedal mass. They penetrate into the massive foot muscle, running parallel and centrally, throughout almost its entire length. They are separated by a thin strip of muscle enclosing the median venous sinus. Throughout their whole length they have a deep lateral groove and the pedal artery is lodged in it (Text-fig. 25). Each pedal cord is a morphological and histological entity and is richly provided with external nerve cells.

[DISSECTION. It is necessary to find the whole of the pretorsional left visceral connective and the abdominal ganglion, together with its branchial ganglion and the

right hand dialyneury, before the huge shell muscle can be cut away to dissect the pedal cords in the underlying foot muscle (fig. 20). Trace this visceral connective up from the floor of the anterior visceral chamber. It adheres closely to the left anterior border of the shell muscle, where it gives off a short branch, swelling into the branchial ganglion. This lies in the mantle lobe attached to the left border of the shell muscle. Find the anastomosis, which passes from the base of this ganglion through the mantle and the anterior border of the shell muscle to join the right pallial nerve and penetrates partly in the shell muscle to reach the right side of the mantle. Follow the remainder of the post-torsional, right visceral, connective which skirts the left side of the shell muscle and then passes over the middle visceral region. Cut off the mantle from the shell muscle, keeping all but the mantle intact (fig. 20). Pin it over to the left and cut off a large portion of the shell muscle. The correct level can be judged by the position of the pleuro-pedal ganglion mass. The dissection of the pedal cords is commenced from the pleuro-pedal ganglion mass. The accompanying pedal arteries and venous sinuses make dissection easier and should be traced at the same time (fig. 14). The transverse commissures and anastomosing epipodial nerves can only be shown in their entirety with laborious dissection. Press up the centre of the foot by padding from below, because the pedal cords lie deeper than the epipodial nerves. The pedal nerves going into the foot muscle arise from the ventral half of the pedal cords and are best dissected from the ventral surface.]

1. *Epipodial Nerves* branch from the dorsal section of the pedal cords, ramifying and anastomosing with one another (fig. 20, *ep.n.*). They innervate the main part of the epipodium with its sensory structures; a branch can be traced into each epipodial tentacle. Each cephalic end of the epipodium has one epipodial nerve from the cerebral ganglion and two from the cerebro-pedal connective. These three anterior epipodial nerves anastomose with one another and with the first of the epipodial nerves arising from the pedal cord, which is close to the pleuro-pedal mass. At the anastomoses there are a few nerve cells. The wide separation of the innervating centres

of the epipodium is doubtless important for co-ordination of the various parts of the body.

2. *Shell Muscle Nerves* occur singly or in twos or threes between the epipodial nerves. They pass up dorsally from the pedal cords and branch to the muscle fibres (*sh.m.n.*). The arrangement of the nerves helps the shell muscle to contract rapidly in response to the stimuli received by the rich sensory structures of the epipodium.

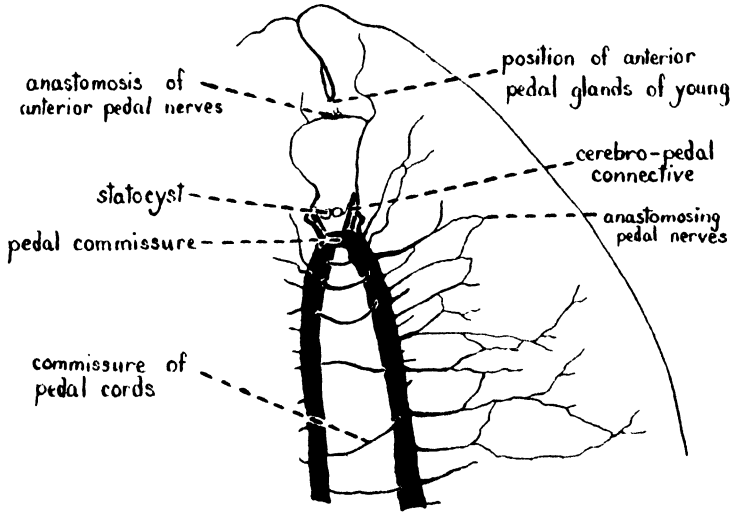
3. *The Pedal Cord Commissures* (*ped.co.*) are fifteen to thirty-six delicate transverse connections between the pedal cords, which resemble the connections in Amphineura. They are erratic in size and are not all in the same plane, but the larger ones are dorsal to the median venous sinus and run in factors of the sinus. Some are oblique and occasionally join one another.

4. *Posterior Pedal Nerves* (*ped.n.*). Numerous nerves pass from the ventral half of the pedal cords and branch into the foot. They are, therefore, more ventral than the epipodial nerves, but are not all in one plane. The main branches anastomose near the margin of the foot sole.

5. *Anterior Pedal Nerves* (fig. 21, *ant.ped.n.*, and Text-fig. 26). These leave the extreme anterior end of the pedal part of the pleuro-pedal mass. They penetrate into the anterior foot muscles, lying ventral to the anterior pedal artery and, like the posterior pedal nerves, they are most easily dissected from the ventral surface. Immediately posterior to the anterior pedal cleft these nerves anastomose and innervate the anterior pedal gland of post-larval specimens (Text-fig. 26). The position of this anastomosis and its importance in connection with the anterior pedal gland have not hitherto been described.

External Pallial (Pleural) Nerves (figs. 12 and 20, *e.pal.n.*). The mantle is mainly innervated by this pair of nerves connected with the dorsal part of the pleuro-pedal ganglion mass, but that region bordering the branchial

cleft has nerves connected with the lateral ganglia of the pleuro-visceral loop. The external and internal pallial nerves anastomose in the anterior lobes, which are extremely sensitive. The external pallial nerves join the pleuro-pedal mass immediately ventral to the visceral cords.



TEXT-FIG. 26. Ventral view of Nervous System. × 3.

The Right External Pallial Nerve is slightly thicker than the left one and its twisted proximal part is covered by a few tegumentary muscles. It penetrates a small anterior portion of the shell muscle, where there is a long right-hand dialyneury (fig. 12). This pallial nerve innervates the right border of the mantle and the mantle pocket which encloses the visceral appendage (fig. 12).

The Left External Pallial Nerve passes to the left beneath the viscera and runs parallel with the visceral cord for a little distance and there is a short dialyneury near the left branchial ganglion (fig. 20, *dia.*). The pallial nerve turns abruptly forward and passes along the extreme left border of the left mantle lobe.

Several minute tegumentary nerves go to the body

wall from the pleuro-pedal ganglion mass, but these are omitted from the diagrams.

Visceral Loop. The pleuro-visceral connectives pass dorsally from the pleuro-pedal mass and make an extensive visceral loop on the dorsal surface of the abdominal viscera. They are flat, have superficial nerve cells throughout, and the three widely separated ganglia are without definite limits. The branchial ganglia are placed symmetrically in the ctenidial supports, at a considerable distance from the pleuro-pedal ganglion mass, so that they can control innervation of the ctenidia and osphradia. The diffuse abdominal ganglion is dorsal (post-tortionally) to the intestine at the posterior limit of the loop. Prior to flexion the rectum would not be posterior to the other viscera and pre-torsionally the abdominal ganglion would be ventral to the digestive system. The median nerve arising from the abdominal ganglion has symmetrical branches, whereas the lateral nerves show asymmetry.

1. **The Right (Supra-Œsophageal) Visceral Cord** (fig. 20, *visc.cor.*).

Near the pleuro-pedal mass this crosses dorsal to the left one, owing to the counter-clockwise direction of the torsion. The cord lies beneath the anterior loop of the intestine. On a level with the anterior end of the large shell muscle it curves dorsal to the œsophagus, to which it gives minute branches. After its dialyneury (*dia*) with the left external pallial nerve, it has a short lateral branch which passes into the ctenidial support, where it swells into the branchial ganglion on the left (morphologically the right) side.

The Left Branchial Ganglion (*br.g.*) lies at the base of the free anterior part of the ctenidium and is equidistant from the osphradium and the ctenidium. The ganglion and its nerves can be seen through the integument.

(*a*) *Efferent Ctenidial Nerve* (*e.ct.n.*). This is parallel and external to the efferent ctenidial sinus. It has

extremely delicate parallel branches arising along its course. They are particularly numerous near the branchial ganglion. Some are very long and the efferent sinus and the sensory epithelium of the ctenidial leaves are innervated by them.

[Slit up the efferent sinus to see the delicate branches, which can be dissected with needles.]

(*b*) *Osphradial Nerve* (*os.n.*). A little thicker than the respiratory nerve, this nerve runs immediately under the yellow osphradium, extending along the whole free border of the ctenidial supporting membrane. It anastomoses with the ctenidial nerve at the tip of the ctenidium.

(*c*) *Left Internal Pallial Nerve* (*i.pal.n.*). It arises at the visceral cord side of the ganglion, runs parallel with, but deeper than, the osphradial nerve until it leaves the ctenidial support and passes into the left mantle lobe, where it aids the external pallial nerve in innervating the anterior part of this lobe. Lacaze-Duthiers first described an anastomosis of these two nerves and of the pair of internal pallial nerves. An important branch curves posteriorly around the margin of the mantle bordering the cleft and joins with its counterpart of the right side at the posterior extremity of the cleft. From this anastomosis, a branch runs in the posterior pallial cleft tentacle. Small nerves pass from the internal pallial nerves of each side to the corresponding anterior pallial cleft tentacle, to the mucous gland and to the border of the mantle.

(*d*) *A Tegumentary Nerve* (*teg.n.*) passes from the posterior part of the branchial ganglion to the neighbouring body wall. It is not important and has escaped previous mention.

(*e*) *The Posterior Portion of the Left* (*topographical*) *Visceral Cord* lies immediately under the integument of the left border of the visceral mass following the mantle

attachment of the ctenidium, not actually in the ctenidial supporting membrane as Fleure stated. Along its course it gives off nerves to the viscera.

(i) Tegumentary and Œsophageal nerves arise along the early part and pass to the œsophageal wall and integument (*t.œs.n.*).

(ii) The Aortic and Pericardial Nerve (*ao.pe.n.*) has a variable point of origin on the cord, but is roughly two-thirds of the distance from the branchial to the abdominal ganglion. It passes through the ctenidial supporting membrane on the left, sends branches, not described before, into the mucous gland and, on reaching the ventral visceral surface, it has branches passing to the aorta and then continues to branch on the ventral wall of the pericardium.

(iii) The left Reno-pericardial Nerve (*pe.ren.n.*) leaves the visceral cord fairly near the diffuse abdominal ganglion. In its origin it is symmetrical with the right pericardial nerve, though its distribution is not exactly the same. Its first branches innervate the modified left renal organ. A second nerve runs in the left anterior and ventral walls of the pericardium and ventricle. A third and final set of branches roughly corresponds to the whole pericardial nerve arising from the visceral cord on the right. These two nerves innervate the remainder of the pericardial wall and the two auricles. The pericardial nerves are variable; sometimes there are additional small ones arising further in the abdominal ganglion than the two main nerves, which then have compensating reduction.

2. **The Left (Infra-Œsophageal) Visceral Cord** (*visc.co.l*). From the pleuro-pedal mass this cord soon passes ventral to the right visceral connective and rises up the concave left anterior border of the large shell muscle. The dialyneury is from the visceral cord side of the branchial ganglion, passing in the anterior shell muscle attachment of the mantle to the right external pallial nerve at its exit from the muscle on to the mantle.

The Right (*pre-torsional left*) *Branchial Ganglion* is symmetrical with the one on the left and has corresponding nerves.

(*a*) *Right Internal Pallial Nerve* (*i.pal.n.*) branches earlier than the one on the left side into the anterior mantle lobe nerve and the mantle border nerve innervating the right side of the mantle cleft. Its branches have been described with those of its counterpart on the left.

(*b*) *The Posterior Portion of the Right* (*topographical*) *Visceral Cord* follows the junction of the visceral wall with the left edge of the shell muscle and lies immediately under the integument, but curves gradually to the left to meet the left visceral connective in the abdominal ganglion, which is slightly displaced to the right. The nerves of this right section are not symmetrical with those on the left, because of the asymmetry of the organs in the flattened visceral hump.

(i) One or two small tegumentary nerves are not figured.

(ii) A small nerve passes into the right renal organ (*ren.n.*).

(iii) A large and extensive genital nerve (*g.n.*) passes beneath the posterior attachment of the right ctenidium and then runs very superficially just posterior to the shell muscle, to which there are small branches; its continuation into the visceral spire, with branches to the conical appendage and stomach, etc., can be followed through the transparent integument. By these nerves, the digestive gland, crop, stomach, and cæcum are innervated. (The anterior parts of the digestive system are innervated from the buccal and labial commissures.)

(iv) The right pericardial nerve (*r.pe.n.*) innervates the right side of the pericardium and right auricle, but has a small branch passing over the right renal organ and terminating in branches to the left side of the digestive gland and intestine.

Abdominal Ganglion (*abd.g.*). This third ganglion on the

visceral loop is diffuse and is dorsal (pretorsionally subintestinal). It lies a little anterior to the posterior end of the right ctenidium, to which it is nearer than to the left ctenidium.

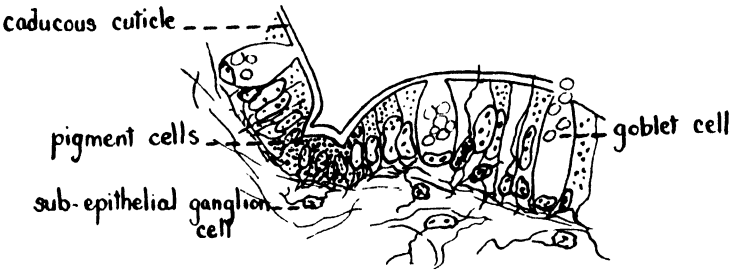
The rectal nerve (*rect.n.*) is its most important unpaired nerve, with symmetrical branches. It curves from the posterior end of the ganglion up to the ventral surface of the rectum. The intestine has bent forward during early larval flexure, so that it is in the mantle roof, overlying the middle visceral region. The rectal nerve passes over the basi-branchial sinus, where it gives off a pair of nerves with branches to the afferent ctenidial vessels and renal openings (*aff.*+*ren.n.*). Pelseneer, 1898, has priority in the discovery of the afferent vessel nerves in *Fissurella* and *Haliotis*. These are omitted by all other authors, who assume that this vessel is innervated from the ctenidial nerve along with the efferent sinus. The rectal nerve continues anteriorly, ventral to the rectum, and is embedded in the pleats of the mucous gland. There are branches to the rectum here, as shown in fig. 20.

SENSE ORGANS.

The whole integument, including all the surface of the mantle with its glands, has general sensibility. This is due to the presence of neuro-epithelial cells between the glandular and supporting epidermal cells. These sensory cells may be scattered, or collected into buds in regions with special tactile or chemical perception. The cells are plentifully distributed in the pedal sole and pedal gland region, in the ctenidial lamellæ and in the margin of the mantle. In this way local movements and exudation of mucus are controlled.

The neuro-epithelial cells are in groups on the head pleat, on the lips and the mouth opening (" taste buds "), and large collections of them are found in the special sense

organs of the head and elaborate epipodium. Patches of the darkly pigmented integument are sensitive to light (Text-fig. 27). *Haliotis* is very sensitive to shadow movements, and those produced by a dissecting needle, but not the vague ones from a glass rod, cause the animal to retract into the shell as much as possible. The ability to seek out dark crevices in rocks seems important in its habit of life. *Haliotis* is also very sensitive to water vibrations. A simple sub-epithelial nerve plexus connects with all neuro-epithelial cells, which frequently have sensory terminations penetrating through the cuticle.



TEXT-FIG. 27. Dorsal pedal epithelium. ×800.

Specialised neuro-epithelial cells are aggregated into definite sense organs, which are exceptionally profuse in *Haliotis*. It is almost impossible to distinguish experimentally between the sense of taste and the olfactory sense in marine animals. My observations show that the cephalic, mantle, and epipodial tentacles and the osphradium appreciate even slight chemical changes in the water. In all the tentacles this sense only extends for 2 to 3 cm., but in the cephalic tentacles of carnivorous molluscs the range is longer. In all tentacles the sense of touch is particularly acute. The very numerous epipodial tentacles are used for investigation of the environment in the same way as the cephalic tentacles. They are particularly useful to *Haliotis*, with its habit of cramming

itself either backwards, forwards or sideways into small crevices between rocks. The epipodial hillocks are also tactile and olfactory, but the latter sense is specially located in pits on the ventral surface of the epipodium. Sunken lines on the cephalic tentacles, and spots in the dorsal surface of the pedal epithelium, are possibly accessory organs of sight for the lateral regions. The two eyes have very highly modified neuro-epithelium which is in an open cup, contrasting with the closed one of most Rhipidoglossa. The statocysts are well-developed orientating organs. New observations concerning the various sense organs are given in the following descriptions.

A. TENTACLES (figs. 26-27).

The position and appearance of the cephalic, mantle, and epipodial tentacles is already described under External Features. Histological and physiological details are given here.

The cephalic tentacles may stretch out to a length of 10 cm. in average-sized *Haliotis*, but in smaller animals they are proportionally more extensible (fig. 1). The larger epipodial tentacles reach almost as far, but the mantle tentacles are decidedly shorter. When creeping, the animal waves the cephalic tentacles upwards and forwards and in a " fumbling " manner ; it touches the rocks and weeds with the extreme tip and then, with the anterior sixth part of the tentacle, it strokes over the rock surface, often sweeping towards its body. The tip of the tentacle is probably the region of maximum sensitiveness. On the dorsal surface of these tentacles there is a longitudinal darkly pigmented stripe. This has closely packed cells with very dark green pigment granules, which are larger and more numerous here than in other parts of the tentacular epithelium. The cuticle is also slightly thicker than elsewhere (fig. 27, *cu.*). The histological evidence in *Haliotis* favours the possibility of perception of light and dark by the tentacles.

With the exception of the stripe on the cephalic tentacles, the whole surface of all tentacles is covered with small papillæ. It is usual in Diotocardia for the sensitive surface of the tentacles to be increased by such papillæ. In the youngest creeping *Haliotis*, only 2 to 4 mm. long, the movements of these tentacles can be watched microscopically. Because the tentacles in these small specimens have scanty pigment, it is possible to use vital stains to help elucidate the types of epithelial cells. When the tentacles are extended, the papillæ are almost at right-angles to the length of the tentacle (fig. 26). They are contractile, owing to fine muscular strands (fig. 27, *m.f.*).

In sections there are closely-packed sensory and supporting epithelial cells, with scattered mucous cells. The sensory cells are very highly specialised. Their nuclei stain much more darkly than those of the supporting cells, which are oval and more transparent (fig. 28, *su.c.*). The sensory cells are often spindle-shaped, with the finely granular nucleus placed deeply in the papilla and with distal processes ending in stiff bristles, which penetrate through the cuticle (figs. 27 and 28, *bri.*). Flemming, 1883, called these " Pinselzellen " and he held the opinion that the papillæ resemble taste buds of Vertebrates. My observations show that sensory cells respond to chemical changes in the water. The stiff hairs are short on the lower parts of the papillæ, but, at the blunt tips of the latter, they are long and are arranged as a circular fringe like a sweep's brush. In *Incisura*, Bourne describes the sensory cells of the papillæ each with one stiff short cilium. Long delicate processes from sub-epithelial nerve cells connect with the sensory cells and have fine processes continuing through the cuticle to the external surface. The nerve cells have processes passing to branches of the tentacular nerves (figs. 27 and 28, *sen.c.n.* and *t.n.*). These processes can be seen after Flemming fixation, without acetic acid, and staining with iron hæmatoxylin and

orange G, but are better seen with the Ranvier-Lœwit method for nerve endings.

The supporting cells are columnar, with green-brown pigment granules, similar to those of the general integument. They have minute processes holding them to the basement membrane, close under which is the sub-epithelial nerve plexus.

Globular mucous cells are larger than those in the general integument and lubricate during the stroking movements of the tentacles. The cuticle covering the tentacular epithelium shows up in yellow with picro-carmine.

Throughout the length of the tentacle there are fine ramifying nerve threads carrying sensory impulses from the sub-epithelial plexus to branches of the large tentacular nerve, which is slightly eccentric and lies ventral to the tentacular artery. Other fine branches pass from the tentacular nerve to innervate the muscles, so that sensory and motor fibres are mixed. In longitudinal sections the main nerve shows undulations, owing to contraction of the muscles. The tentacular nerve arises in the central region of the cerebral ganglion. It is ganglionated for a considerable distance and even distally to the yellow ganglion swelling, at the base of the tentacle.

When the epithelial cells are removed, after maceration in potassium bichromate, muscle processes of the papillæ stick out like spikes. The fibres are mainly longitudinal and oblique, so that they are retractors of the papillæ. In the central part of the tentacle the muscles are mainly in longitudinal bundles, which retract the whole tentacle. Stretching between these are branching transverse bands of muscle. In a state of tonus they make the tentacle thinner and, aided by blood-flow into the loose connective tissue, they extend the tentacle (fig. 27, *m.l.*, *m.tr.*).

The tentacle artery (*t.a.*) runs longitudinally in the central part of the tentacle, but is displaced towards the

dorsal stripe. A peripheral circle of lacunæ (*lac.*) runs parallel with the artery and a larger space surrounds the tentacular nerve. This connects at the base of the tentacle with the hæmocoele of the cephalic region.

As is usual in Mollusca, tactile and chemical senses are far more active than the sense of sight. All three senses may assist *Haliotis* in finding its preferred seaweeds. Gentle stimulation with glass "silk" produces local reaction, but heavier stimulation gives general reaction. The reaction seems similar to that which Dakin found with Anemones. My observations show that the tentacles of *Haliotis* are sensitive to differences in temperature. This can be demonstrated by warming the surrounding water with a hot needle.

The three pallial cleft tentacles are smaller, but have the same structure as the cephalic tentacles. They are innervated by branches of the internal pallial nerves. (See Nervous System.) By their tactile and olfactory perception, they may stimulate approximation of the margins of the mantle bordering the cleft, to bring about closure of the shell perforations for protection of the ctenidia. They seem also to help to preserve the shell orientation, so that the shell holes remain over the pallial cleft. When the shell is removed, they fumble upwards and sideways in an agitated manner. They keep the shell perforations clear for the escape of deoxygenated water with genital and excretory products.

B. THE EPIPODIUM is more elaborate in *Haliotis* than in any mollusc. It is a dorso-lateral development of the foot and its profuse and varied projections have been mentioned with the external features. When outstretched, these can receive impressions from a very large area of the surroundings. Other molluscs probably make up for this by increased sensitiveness of the mantle edge.

The elaborate innervation of the epipodium was described with the Nervous System (fig. 20).

Anastomosing nerves from the cerebral ganglia, cerebro-pedal connectives and pedal cords have delicate branches running through the centre of the epipodial tentacles and other sensory epipodial structures.

The epipodium is well supplied with oxygenated blood, which discharges from the pedal arteries into lacunæ in the epipodium and is returned by large venous sinuses. These are very obvious in horizontal sections, lying between the muscles at the junction of the foot and epipodium. The structure of the countless epipodial tentacles is the same as that already described for the cephalic and mantle tentacles. Like the latter, they appear to be concerned in orientating and cleaning the shell. I observed that the epipodial tentacles are constantly feeling up over the margin of the shell. This is noticed particularly just prior to sudden alteration of the position of the shell. In minute specimens the mobile edges of the epipodium are frequently swept over a considerable part of the shell, probably for cleaning it. Within a few minutes after shell injury, the epipodial tentacles stretch over to investigate even as far as the border of the hypertrophied shell muscle. I have also observed them helping the conical appendage to squirm back into the mantle pocket when it has slipped out after shell removal. Like the cephalic tentacles, these epipodial tentacles sweep over the surrounding surfaces and may assist in finding food and suitable lodging. When *Haliotis* has fallen shell downwards, all tentacles assist in working out the suddenly changed topography, in preparation for complete turning over. After contraction, due to irritation, the anterior epipodial tentacles usually extend before the cephalic tentacles to commence investigations.

Ventral to the bases of the cephalic and epipodial tentacles there are very definite, ciliated, cream coloured areas, which are specially well developed beneath the ventral epipodial fringe, and show plainly against the

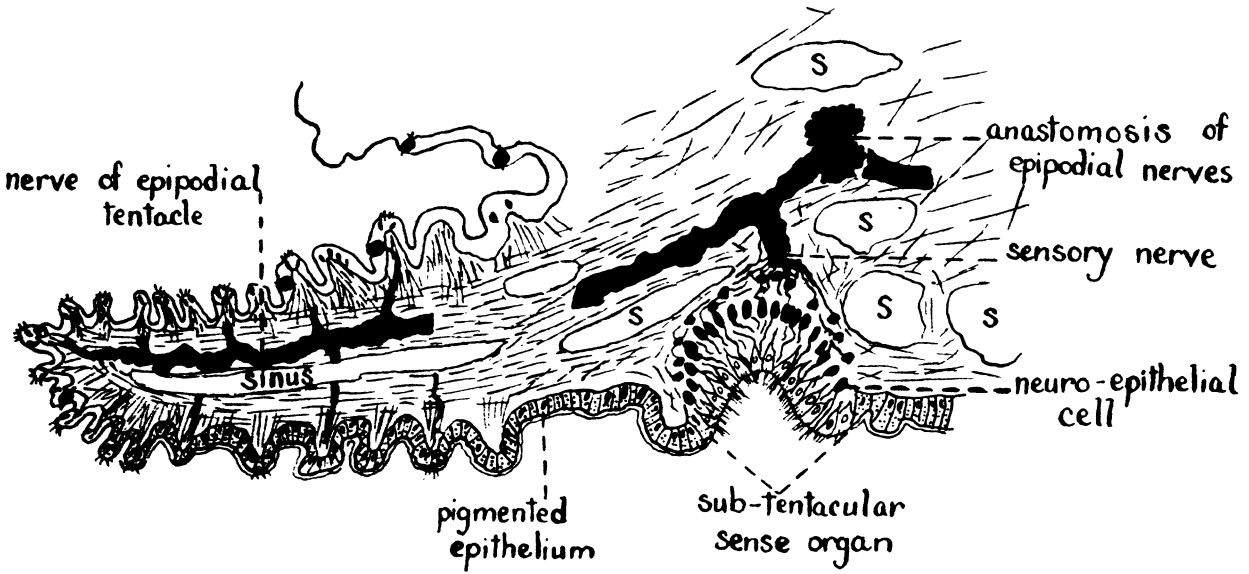
darkly pigmented neighbouring parts. These epipodial areas were first described by Thiele, 1890, as sense buds or side organs. Simroth has compared them with lateral line sense organs of fishes. Those under the cephalic tentacles have not been described by other authors. They are probably sensitive to chemical stimulations.

In structure they resemble the osphradia. The epithelial cells may be 30μ in height, so that it is easy to distinguish them from the much lower surrounding cells of the integument. The nuclei are arranged in two rows, but I do not agree with Thiele that the inner ones belong to supporting cells. They are elongated, stain darkly, and in every way resemble the nuclei of neuro-epithelial cells. Their long sensory processes terminate as fine surface processes (Text-fig. 28). Internally these sensory cells have connecting processes with sub-epithelial ganglion cells, which connect with a special nerve branch arising from the anastomosis of epipodial nerves. The distal cells are ciliated supporting cells.

As Thiele pointed out, these areas can be bulged out or retracted into a depression.

The hillocks covered with papillæ, which are characteristic of *Haliotis tuberculata*, lie in the area between the epipodial fringes. Their colour and arrangement was described with the external features (fig. 6). They are similar in structure to the tentacles but are less extensible and there are no terminal brush cells to the papillæ. Ordinary neuro-epithelial cells and large round ones with large spherical nuclei are present. The latter cells are also among the epithelial cells of the picot-edging of the epipodial fringes. Possibly these are gustatory cells.

Minute white spots are scattered among the pigmented parts of the ventral surface of the epipodium and on the dorsal pedal integument. The olive brown and black pigment of the surrounding cells vanishes very suddenly around the margin of the spot, which is somewhat sunken. The cells are low, with nuclei sometimes elongated parallel



TEXT-FIG. 28. Sub-epipodial sense organs. ×300.

to the surface. They appear to be unciliated and have transparent cuticle, as in other parts of the integument. They may be part of the protective colouration, resembling *Spirorbis*, but possibly they have a sensory function, such as perception of vibrations in the water.

C. OSPHRADIA (figs. 25, 17, and 20).

These were first described by Spengel in various molluscs, including *Haliotis*, as organs of smell. Bernard has given some description of them in *Haliotis*. They are paired and placed symmetrically at the entrance to the respiratory cavity, so that they are in a suitable position to examine the water before it is used for oxygenation of the blood in the ctenidia. In the presence of foul water the respiratory chamber is closed by the retraction of the shell and mantle edges. The osphradia are represented by a long ridge with a central pleated groove passing along the whole free edge of each gill support and I find they continue for more than the same distance along the ctenidial support inside the ctenidial chamber (figs. 17 and 20). Because of the pleated groove Wegmann suggested they are accessory ctenidia. The osphradia are easily seen by their yellow-green colour.

The pleated groove increases the area of sensory epithelium. The cells are very tall and closely packed. The epithelial cells have numerous cilia, which are only about one-eighth the length of those on the ctenidial lamellæ. The ciliated cells act as supporting cells to the numerous sensory cells; these are wedged between them with their nuclei lying in irregular positions, but usually internal to the ciliated cells. They are so closely packed that they extend for a considerable depth. These sensory cells have elongated processes connecting with sub-epithelial ganglion cells, whose fibrils continue proximally into the osphradial nerve with its ganglionated sheath. The nerve is closely connected with the ctenidial nerve, both distally and proximally (fig. 20).

The sensory cells have peripheral processes among the

ciliated cells. Small mucous cells sometimes protrude above the ciliated surface.

Thiele described sensory stripes continuing from the osphradia and passing round the anterior borders of both hypertrophied right shell muscle and reduced left shell muscle. He called these sub-pallial sense organs and considered them to be connecting links between the outer pallial lobes and the respiratory cavity.

D. EYES (figs. 1 and 24).

Each eye is seen superficially as a black spot at the tip of each of the pair of optic tubercles, which are placed externally to the cephalic tentacles. These cup-shaped structures are not closed by cornea and in this respect resemble those of the Docoglossa, but they are much better developed than in such of its members as *Patella* and have a crystalline lens.

The members of the Rhipidoglossa are generally believed to have distinct retinophoræ and retinulæ in the retinal epithelium. With regard to this specialisation of the retinal epithelium, my observations do not agree with those of any previous author, including Fleure. It is impossible to agree with Patten and Hesse that the optic cup is closed. The eyes are more primitive in structure than has been supposed.

The retina is formed from a goblet-shaped invagination of the tegumentary epithelium, with the margin drawn in to leave a small external aperture, so that water can bathe the vitreous body, which is secreted into the cup by the retinal cells.

The histology of the eye can be described under the headings retinal epithelium, innervation of the retina, and accessory structures.

1. **The Retinal Epithelium** is only seen satisfactorily in median vertical sections of the ocular tubercle, which are cut not more than 6μ in thickness. Fleure and Hesse found *Haliotis* material unsatisfactory for the histology

of the eye, but it shows reasonably well after Bouin fixation or with Flemming without acetic acid, and iron-hæmatoxylin or picro-indigo-carmine are satisfactory stains.

All the retinal cells have pigment granules and probably are sensitive to light and all help in the secretion of the accessory layer of rods and the vitreous body. Therefore there is no sharp differentiation of the sunken epithelial cells of the cup into retinophoræ and retinulæ, such as previous authors have described. There are, however, two types of cells, which are not clearly distinct. Both kinds are very elongated and narrow. The long nuclei vary in position from almost basal to nearly half the height of the cell. The cells with more basal nuclei resemble retinophoræ of other Gastropoda in the presence of light refracting granules, but distally they also have black pigment granules (fig. 24). Proximally these cells taper into one or two threads, which pass through the basement membrane and are connected with ganglion cells lying beneath it, but some nerve cells penetrate between the shrunken nucleated ends of the retinal cells. Their fibrils anastomose with those of other ganglion cells and processes pass distally between the retinal cells. Occasionally the epithelial cells have two nuclei owing to the process of cell division or they are possibly fused cells.

The other retinal cells resemble retinulæ and their dense black-brown granules are packed into heaps in the whole distal half of the cell. These retinal cells also have ganglion cell connections and there are intermediate cells between these two types. The retinal epithelium gradually lessens in height as the opening of the optic cup is neared.

2. **Innervation.** The sub-retinal ganglion cells are multipolar and one cell may innervate two epithelial cells of the retina, or two or three ganglion cells may connect with one epithelial cell. Sensory nerve fibres pass eventually to the optic nerve, but there is an elaborate

network of anastomosing branches surrounding the retinal cup and the branches do not collect into the optic nerve for some distance (fig. 24, *opt.n.b.*). This network was first shown by Lacaze-Duthiers. There is a similar arrangement in *Trochus*. The optic nerve also has motor fibres running to the muscles of the tubercle. It passes to the dorsal central region of the cerebral ganglion and, according to Thiele and Fleure, its fibres can be traced to the origin of the cerebro-pleural connective.

3. **Accessory Structures.** The retinidian layer and the crystalline lens are secreted by all cells of the retinal epithelium. Some previous authors state that the " colourless " retinophoræ are alone secretory.

(*a*) *The retinidian layer* is a layer of poorly developed rods, each made of a bunch of fine straight fibrillæ, which are narrow cuticular outgrowths from the retinal cells (*ro.*). They are transparent and refractive and their rounded distal ends lie in the homogeneous refractive body.

(*b*) *The crystalline lens* is a spherical body, surrounded by a less dense layer, which is sometimes called the vitreous body. It is a hyaline cuticular structure which appears at the external aperture and can be bathed by water, because the ocular cup is not closed by a cornea as it is in most of the Rhipidoglossa and in higher Gastropods. In minute specimens, examined in living condition with a 1-inch objective, the crystalline lens appears to bulge outside the aperture of the cup, when the optic tubercle is fully extended. It is firmer in older animals and the surface is hardened by sea water.

(*c*) *The musculature* is similar to that of the cephalic tentacles, but is more irregular. The muscles are innervated by optic nerve strands arising at various levels throughout the optic tubercle.

(*d*) *The blood supply* is by a small artery having a common origin from the cephalic aorta with the tentacular artery. It runs almost centrally, following the optic nerve.

(*e*) *Specialised tegumentary epithelium* borders the small external aperture of the cup. The cells are quite six times as high as those on the remainder of the optic tubercle, and there are many sensory cells. When tested with finely drawn-out glass threads, this region appears to be very sensitive to touch and closes over the crystalline lens for protection. The optic tubercle contracts at the same time. This specialised epithelium is first recorded here.

My observations show *Haliotis* to be exceedingly sensitive to the impact of shadows, even when the eyes are covered. Probably dermal perception is made possible by pigmented cells covered by transparent cuticle (Text-fig. 27).

E. Statocysts (figs. 21 to 23).

These organs of orientation are also ectodermal in origin and develop at an early stage with the nervous system. In *Haliotis* they retain their primitive attachment to the anterior surface of the pleuro-pedal ganglion mass, although the static nerve passes to the cerebral ganglion. In pelagic Gastropods the statocysts have migrated into the vicinity of the latter nerve-centres. In specimens 2 mm. long the statocysts and pleuro-pedal nerve mass still lie very near the anterior end of the pedal sole and they and the whole nervous system are relatively large. Fleure considers that the slight bulge in the lateral wall of these vesicles, lying near the static nerve, is a vestige of the embryonic connection with the exterior, as is shown in Cephalopods. It is, however, larger in old specimens than in young ones, and the epithelium readily breaks at this point.

The statocysts of the smallest specimens lie close to the ganglion mass, and are only separated from it by a continuation of the thin sheet of connective tissue, which envelops the whole nervous system. In older specimens a considerable amount of gelatinous connective tissue surrounds the statocysts and presses them apart. There

are stellate connective tissue cells and some large plasmatic cells scattered in the connective tissue.

The position of the statocysts, lying immediately above the pedal muscles, ensures protection. Each is slung up by three delicate muscles inserted on the connective tissue capsule (fig. 21 and Text-fig. 25). An anterior muscle is small and passes round the buccal muscular mass to the head wall, a short lateral muscle connects with the connective tissue sheath, dorsal to the origin of the cerebro-pedal connective and with the connective tissue surrounding the œsophageal pouch. A more obvious dorsal muscle passes vertically to the muscular wall of the cephalic aorta, which forms a roof over the pleuro-pedal nerve centre and attaches to the base of the anterior end of the hypertrophied shell muscle.

The statocysts are hollow vesicles, which are usually spherical, but sometimes dorso-ventrally flattened. They are lined by epithelial cells, with a rich supply of neuro-epithelial cells and contain colourless fluid in which float numerous concretions of calcium carbonate.

The statocyst epithelium consists of small very delicate cells, which crush easily in fresh condition. Lacaze-Duthiers was unable to find their cilia, but Fleure stated that the cells are ciliated. After careful examination of living cells and of sections of statocysts removed for fixation, it seems probable that there are three types of cells. The most numerous are elongated cells with a few stiff cilia which cling together like hairs of a paint brush. With high magnification these can be seen moving the statoliths inside a statocyst, which has been slightly crushed under a coverslip. The cytoplasm of these cells is dotted with minute straw-coloured granules. Among these cells are neuro-epithelial cells with much less cytoplasm and nuclei, which stain darkly in sections. They taper to long hair-like processes, which project into the fluid of the vesicle and resemble hair cells of the sensory ampullæ

of fishes. The processes are sometimes branched near the extremity. These hair cells are scattered, so that there is no special " macula " region, such as the statocysts of more highly specialised Gastropods possess. There are also larger glandular cells, which can be found discharging new statoliths into the cavity. They probably also secrete the fluid. All cells are very broad in young statocysts.

The statoliths vary much in size and may be spherical or oval. They appear to have a centrum, surrounded by concentric growth marks. In a specimen of *Haliotis* only 8 mm. long the largest statoliths showed three growth rings, but the smallest had none.

Innervation. The static nerve passes from the lateral wall of each statocyst in a posterior direction, then curves outwards round the pleuro-visceral connective and travels up to the cerebral ganglion in company with the cerebro-pleural connective. (*Vide* Nervous System.)

The nerve plexus connecting the sensory epithelium with the static nerve is best seen after prolonged vital staining with methylene blue (fig. 23).

Numerous sub-epithelial ganglion cells connect with external processes of the sensory cells. These are dotted along the course of fine nerve strands, which have large terminal cells staining darkly. These fibres collect together to form the static nerve and, where this leaves the statocyst, there are many ganglion cells.

Differences in orientation are perceived by movements of the statoliths against the sensory cells and the impulses are conveyed via the ganglion cells and static nerve to the cerebral ganglion. The muscle strands preserve the normal position of the statocysts.

MUSCULAR SYSTEM.

The muscles in *Haliotis* form a considerable part of the body. The muscle fibres are elongated and oval in section. They may be 15μ by 1μ and, in the buccal mass, they have marked transverse striations.

The most obvious muscular regions are the continuous mass of the hypertrophied right shell muscle and the foot, together with its epipodium. This mass makes a horizontal plaque with the right shell muscle standing vertically as a central oval pillar. The muscles are very closely packed, particularly in the pillar, so that only small irregular lacunæ lie between the muscle bundles. The latter run mainly in vertical direction from the shell muscle into the foot (fig. 37). They are covered dorsally only by very flattened epithelial cells firmly adhering to the centre of the flattened shell and they form a very powerful adductor shell muscle. When *Haliotis* is in the normal suspended position the weight of the shell would be against adhesion, particularly when out of the water, and the central position of fixation of the muscle has a mechanical advantage. The muscle, when in a state of tonus, makes the vacuum. The hypertrophy of the right shell muscle and extreme smallness of the left is an advantage in an animal with much flattened shell, for it can lift up the shell with the visceral mass from the pedal mass and twirl it about, while trying to wedge the body into crevices, and it can move the foot and epipodium in a similar flexible manner to turn over after falling with pedal sole uppermost. The small left shell muscle attaches firmly to the anterior end of the shell flange, which is held in its posterior region by the double mantle edge, so that the mantle cavity is open only anteriorly and to the right.

In Gastropods with conical shells, like the limpet, the retracting shell muscle is a symmetrical horseshoe, instead of a columellar muscle passing through the spire of the

shell as in typical Gastropods. (See Embryology.) It is possible that the huge shell adductor of *Haliotis* is the hypertrophied right extremity of a post larval horse-shoe muscle, and the small left muscle is its left extremity. In the young creeping stages muscle fibres are very clearly seen, connecting the two shell muscles beneath the visceral mass (fig. 37). Simroth considers that the columellar muscle has migrated from the spire, where it is in *Pleurotomaria*, to the new central fixation on the last shell whorl.

The epipodium has a considerable number of horizontal muscle bundles which serve to retract the epipodial collarette. The integument is supported by sub-epithelial interlacing muscles.

The visceral mass is held in position by ventral muscles passing to the ventral mantle plate (fig. 14, *mant.pl.m.*) and by short dorsal muscles from the posterior end of the hypertrophied shell muscle. The buccal mass is held in position by the muscle strands radiating to the various parts of the head wall and to the dorsal surface of the foot.

The odontophore muscles have been described with the digestive apparatus. They are strongly striped and are pink, owing to the presence of hæmoglobin. Blanchard first pointed out the striations in *Haliotis* and *Pecten*. In his description of *Incisura*, Bourne has added to the knowledge of the histology of these muscles. Each fibre is a single tapering cell with its nucleus at the broad end. There is a central core of unmodified reticular protoplasm enclosed in a sheath of contractile substance, which produces the striations. The whole is invested by a delicate sarcolemma. The contractile substance is thick only in two bands following the ends of the long axis of the oval, which is seen in transverse section. In surface views of the fibres the striations are therefore sometimes missed. According to Bourne the structure supports the reticular theory of constitution of striped muscle fibres.

In the right renal organ there are a number of muscular

supports (fig. 31, *m.f.*). Muscles are absent in the left renal organ except under the dorsal integument.

The muscles of the ctenidia are described with the respiratory system.

EXCRETORY SYSTEM.

(Figs. 11, 17, 29 to 33, 38, 39, and Text-figs. 22, 29 and 30.)

A pair of renal organs is present. This is yet another remnant of the primitive symmetry, but the organs are very unequally developed and differ much in structure and in physiology. They lie one on each side of the pericardium and the external renal openings are on each side of the hypobranchial portion of the intestine. The excretion is discharged into the respiratory chamber and escapes mainly through the shell holes.

As in the Amphineura, two renal organs are present in all members of the Aspidobranchia, with the exception of the Neritacea, but in no case is the ancestral symmetrical arrangement of these organs and of the genital glands preserved. In *Haliotis* the post-torsional right renal organ is very large and excretes solid and liquid products, with much uric acid, which is characteristic of Gastropod excretion, whereas the left renal organ is reduced and changed to a papillated sac, which has a modified renal function together with probable newly acquired functions.

The work hitherto published on the renal organs of *Haliotis* and other members of the Aspidobranchia is so contradictory that the cytological and physiological details demanded special investigation. The homology of the renal organ of mononephridial Gastropods with one or other of these organs in Zygobranchiate Aspidobranchia has long been a subject for controversy.

Lankester's view is that the single organ of the majority of Gastropods is homologous with the post-torsional left organ in binephridial forms. According to Perrier, the

solitary kidney in Pectinibranchia is homologous with the post-torsional right organ in Aspidobranchia. The former view is most favoured since the investigations of Erlanger, Pelseneer and Fleure, and the embryological evidence brought forward by Erlanger and Drummond concerning *Paludina*. Haller's support of the second view is based on mistaken observations.

The reduction of the topographical left renal organ in *Haliotis* and the shedding of genital products of the single gonad into the right renal organ corresponds with the arrangements in *Patella* and *Trochus*, except that the gonad discharges directly to the urocœle without a genito-pericardial duct and in this respect *Haliotis* is less primitive (fig. 31 and Text-fig. 22). Following Lankester's view it is argued that the distal portion only of the right renal organ persists in dextral mononephridial forms and is transformed into the gonaduct.

Lankester, Goodrich, Cunningham and others have shown that *Patella* and possibly *Trochus* and *Scissurella* have preserved the reno-pericardial canals of both sides, as in the supposed common ancestors of the Gastropods, Lamellibranchs and Scaphopods. In *Haliotis* the post-torsional left reno-pericardial canal is very noticeable and my experiments with living animals show that its strong ciliary current undoubtedly conveys the excretory pericardial fluid to the left renal cavity and finally to the exterior through the left renal opening.

After a variety of examinations and experiments my conclusion is that there is very probably no right reno-pericardial canal. (See Reno-pericardial canal with cœlom.) This agrees with the observations of Perrier and Erlanger, but not with the observations of Haller, Totzauer and Fleure. It corresponds with the arrangement in *Pleurotomaria*, as described by Martin Woodward, but in *Emarginula* the right reno-pericardial canal alone persists. Adopting Lankester's view of the homology of their one

renal organ, my suggestion is that the loss of the topographical right reno-pericardial canal in *Haliotis* and *Pleurotomaria* is a reduction, which precedes loss of the right organ in mono-nephridial Gastropods.

The great reduction of the right hypobranchial gland and slight reduction in the right ctenidium may also be in favour of Lankester's view, or may be merely due to compression caused by hypertrophy of the right shell muscle. The right renal organ is extensive and most of the venous blood of the whole body passes through its renal portal system. (*Vide* Circulatory System.) This fact appears to favour Perrier's view concerning the homology of the organ in mononephridial forms.

RIGHT RENAL ORGAN.

[Make an incision in the dorsal wall of the right renal organ a little to the right of the reno-pericardial wall and expose its cavity, as in figs. 17 and 29.]

This gland is much more extensive than one imagines from the small portion which is seen on the dorsal surface after removal of the shell. It lies immediately to the right of the pericardium and is overlapped by the digestive gland. It is usually a much darker brown than the latter; in some specimens it is almost black, but in others it is tinged with red. In mature specimens the anterior part, which lies against the left side of the large shell muscle, is covered, not only by the digestive gland, but by the more superficial gonad. This anterior portion of the renal organ terminates in two lobes, which extend ventrally to the viscera, one as far forward as the anterior end of the shell muscle (*R* 1) and the other almost reaches the buccal bulb (*R* 2, figs. 17, 29 to 31). Posteriorly there are also two lobes, one extending round or under the pericardium, as shown in fig. 29 (*R* 3), the other is a diverticulum from this, which penetrates under the digestive gland and lies dorsally to the crop (*R* 4). The extremities of the lobes are thin plates of glandular

tissue. The full extent of this renal organ, with its lobes, has not been described by previous authors.

The gland is very spongy, with a cavernous appearance due to intricate intuckings of the glandular epithelium lining this cœlomic sac. The walls of a vast network of veins of the renal portal system bulge through the glandular cells into the urocœle. The glandular trabeculæ are held in position by muscle bands from the wall of the visceral mass. The anterior lobe is surrounded by muscles which connect with the wall of the cephalic aorta. The lobes of the renal organ are embedded in patches of lymphoid tissue. There is no "ureter." The renal cavity narrows to a pouch with a simple wall, lying ventral to the pericardium and from here the excretion is emptied directly to the respiratory chamber by a button-hole-shaped opening in its posterior roof to the right of the rectum (figs. 17, 29, 30, *r.ren.o.*). This lies immediately anterior to the basi-branchial sinus. The terminal pouch of the right renal organ passes beneath the mucous gland and the rectum and lies close against the wall of the left renal organ. The cavity contains both liquid and solid excretion. Spherical globules with dense brown granules, and genital products during the spawning season, float in opalescent mucous fluid.

The genital gland discharges its contents into this renal cavity by a slit-like aperture, without a gonaduct. The opening is in the dorsal roof of the middle region where the renal wall is very thin (fig. 29, *g.o.*). It is longitudinal in direction and appears to be a wide slit between the gonad and renal epithelium. It is obvious only in mature specimens, but is not open only during the spawning period as other writers have stated. In the accounts of early investigators the right renal opening to the exterior was thought to be entirely a genital opening. Contrary to the statements of Totzauer and Fleure the genital gland of *Haliotis* opens directly to the renal cavity without

the intermediation of a pericardial duct, as in some Lamellibranchs and in *Dentalium*.

Evidence for the absence of the right reno-pericardial canal is given with the description of the pericardial cœlom.

The Renal Portal System has been described in the section on the circulatory system. Almost all the venous blood of the body passes by the afferent renal veins to the superficial parts of the right renal organ and is carried away, after removal of nitrogenous waste, by the efferent renal vessels. These lead to one large efferent sinus, which empties into the basi-branchial sinus and from here the blood passes to the afferent ctenidial vessels (fig. 17). Therefore all the blood reaching the ctenidia is devoid of excretory products. Perrier stated that the large anterior efferent renal vein conveys blood in a direct stream, from the abdominal perivisceral lacunæ to the ctenidia, without breaking up in the renal tissues. All my evidence points against Perrier's view. This vessel has the same relation to the renal tissues as the other two efferent renal vessels.

Small renal arteries pass to the central and anterior regions. These are described with the circulation section, but were not mentioned in previous descriptions.

Histology of the Right Renal Organ (fig. 32). In sections the renal connective tissue is riddled with blood lacunæ. Large vessels near the cavity have circular muscles arranged to form a wall. Perrier thought they branched into true capillaries. The connective tissue cells are arranged like an endothelium in places, but most frequently they are far apart and form a bridging network between the renal tubules.

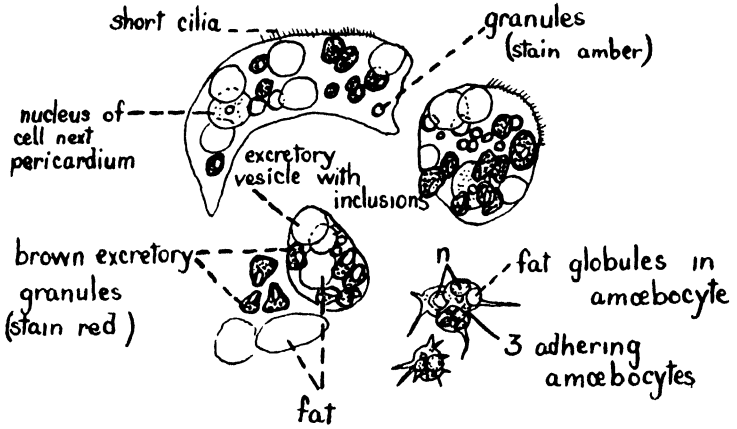
The gland is tubulo-alveolar, not acinous as Haller describes it. The secretory epithelium of the lumen of the organ is folded into slightly branched tubules and frequently the blood channels are close up to the epithelial cells. In sections of animals only 2 mm. to 6 mm. long, it is most easy to follow the arrangement of the walls of the

renal lobes. Here the epithelial wall is simple, except for occasional beginnings of the outpushings of papillæ, which make the very elaborate spongy mass of older animals. In the small specimens the cells are spherical, but they are pressed together to become polyhedral in older specimens. They are held together by hyaline cementing substance. Those cells which lie against the pericardial wall are flattened in the direction of the wall, especially towards the renal orifice. Because of the absence of concordance in previous accounts, details of the cytology of the epithelial cells are given.

The most reliable evidence is obtained from living cells after vital staining, or after physiological injection of weak solutions of trypan blue, neutral red and methylene blue in sea water. This is supplemented by frozen sections and by paraffin sections of animals of various sizes. The most useful stain was methyl-green pyronin of Unna, after Carnoy's fixing fluid. It is impossible to agree with Haller and Perrier that there are greatly varying types of cells giving a high degree of complication for such a primitive member of the Streptoneura. Some of the cells figured by Perrier look extremely like the cells of the digestive gland, which it is very difficult to separate from the renal organ, because minute blood vessels and connective tissues keep the two organs closely united.

The renal cells, however, vary much in appearance according to the state of secretory activity, but I agree with Pelseneer and Fleure that there is no specialisation of the various regions of the organ, except that the cells adjacent to the pericardial wall and lining the cavity of the sac are flat and probably have less depurative function than the cells lining the tubules. Fleure found no cilia, although very short vibratory cilia are distinctly seen on living cells. They are most noticeable on the cells bordering the cavity, but the other cells have probably lost them during their secretory activity. The cilia

probably pass the excretion towards the renal opening, but they are extremely short compared with the very long ones on the epithelial cells of the left renal organ (Text-figs. 29 and 30). The nucleus stains faintly, but has a plasmosome, which stains vivid red after pyronin-methyl-green, and two or three chromatin condensations (karyosomes) are blue-green (fig. 32, *Kar*). In the epithelium lining the cavity the nuclei are near the centre of the cells, but in the tubules they are further away from the lumen.



TEXT-FIG. 29. Living cells of right renal organ, after vital staining with neutral red. ×1,100.

The cytoplasmic granules are usually large and conspicuous because of their deep green-brown colour, which gives the whole organ its brown to black colouration. In cells of mature animals these granules are so large that they are pressed into angular shapes. After vital staining with neutral red, their brown colour is tinged with red, and they are therefore acid, whereas other inclusions turn amber and are alkaline. The granules are most abundant in the tubule cells. In the renal epithelium of post-larval *Haliotis* they are much smaller and spherical. The granules are discharged abundantly into the lumina of the

tubules. They are probably concretions of nitrogenous waste. From the results of histo-chemical tests for inorganic iron, it is concluded that there is much iron scattered in the cytoplasm of these cells. It is possibly concentrated in these pigmented granules. In some cells refractive vacuoles are more numerous than the granules and may run together. After physiological intra-venous injection of dilute acid dyes, such as trypan blue, these vacuoles are coloured. Similar sized drops stain vividly with Scarlet R. The inclusions, therefore, probably contain much fat or lipoids. Sometimes the vacuoles discharge into the secretory cavity, but frequently spherical vesicles of varying size separate off from the cells, carrying off both types of inclusions in their clear cytoplasm. These float and break up in the excretory fluid and have the appearance of small cells, except for the absence of nucleus. Perrier observed this, but I am unable to agree with most of his description.

The blood cells in the venous lacunæ are imperfectly shut off by connective tissue bridges from the epithelial cells, and may press closely against them. When examined in the fresh condition these blood cells have greenish-yellow oily vacuoles and granules which stain with basic vital stains (Text-fig. 29). Nests of large plasmatic cells lie close against the cementing substance of the secretory cells. They have darkly staining nuclei and foamy cytoplasm with granules which stain with both acid and basic dyes (fig. 32). These are the excretory connective tissue cells with excretory function already mentioned with the lymphoid tissues.

THE LEFT RENAL ORGAN.

[Make an incision in the dorsal wall of this organ, which lies between the left hypobranchial glands and the anterior left wall of the pericardium. Cut through the posterior end of the ventricle and the part of the intestine surrounded by it and lift up, or press the ventricle over to the right, to see the left reno-pericardial canal opening to the

pericardium. Pass a bristle through it into the cavity of the left renal organ (figs. 13, 29 to 31).]

This organ is very much smaller than the right renal organ and is much modified in structure. There are so many points of difference that this left gland has probably acquired new functions in addition to its reduced renal function. Haller first named it the "papillated sac" because of the mass of papillæ projecting from its walls into the urocœle (fig. 13, *l.ren.pop.*). The name has been adopted by more recent writers for the same organ in several members of the Rhipidoglossa. Comparison of the macroscopic and cytological features leaves no doubt that this sac in *Haliotis* is almost identical with the papillated sac in *Pleurotomaria*, *Trochus* and *Turbo*. Probably the physiology is the same, but there is contradiction in the interpretation of the structure in all these genera and my observations show that the widely held view concerning the presence of crystals, possibly of protein, is mistaken. Bourne, for *Incisura*, made a tentative suggestion that there is a difference in the left renal organ for the two sexes. He used preserved specimens, including only one male. In *Haliotis* there is no difference in either renal organ for the two sexes.

Further investigation in *Fissurella* seems to be needed, for Perrier has stated that the reduced left renal organ is identical in function with the right organ.

The papillated sac is flattened in antero-posterior direction, because it is wedged between the hypobranchial gland and the pericardium (fig. 31). Unlike the right excretory gland it is a simple sac, although its external opening is symmetrical with the right renal opening, lying on the other side of the rectum. The anterior wall is almost vertical and lies at the posterior limit of the respiratory chamber. The right wall lies partly against the right renal organ. There is, however, no connection between the two renal organs. Fleure and others have

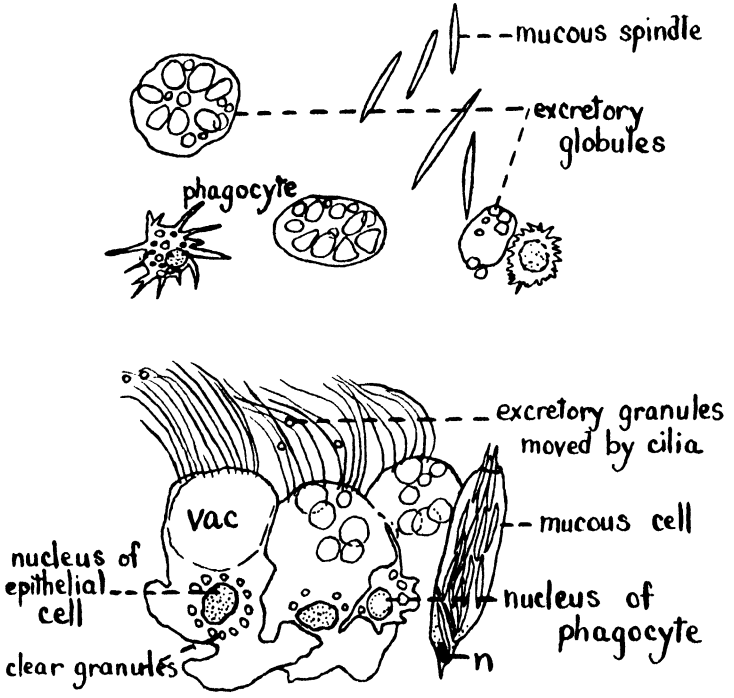
pointed out that Haller's statement, that the papillated sac is merely an attached pocket to the outgoing passage of the right renal organ, is erroneous.

In colour the left organ contrasts sharply with the right organ. It is cream white and the papillæ are translucent, whereas the right organ is brown to black. The papillæ are on all the walls, but are very small on the right wall. They vary in length from 0·5 mm. to 2 mm. and are sometimes branched. They give a bristly appearance to the spacious urocœle.

The position of the left reno-pericardial canal, which brings about the secondary connection of the pericardial cavity with the exterior, is described with the pericardial cœlom (figs. 29 and 31, *l.ren.p.c.*). It is of considerable length and is directed towards the renal opening. Most of the canal has flat pericardial epithelium, but near the urocœle the cells are larger and ciliated. A ciliary current is set up here and on the papillæ, throwing off particles towards the renal orifice. The whole length of the canal can only be shown in horizontal longitudinal sections. There is a valvular arrangement of the papillæ at the renal end of the canal, which doubtless prevents backflow of fluid to the pericardium. From this observation it would seem that Lankester's method of injection from the urocœle to determine the presence of reno-pericardial canals is not good.

The circulation of this organ is peculiar. It is described with the blood vascular system (Text-fig. 22 and figs. 13 and 14). The blood, which passes from the terminal portion of both efferent ctenidial vessels into the vessels of the left renal wall and finally into the large lacuna in the centre of each papilla, is oxygenated and most of it is already freed of excretory products, because all but the small quantity brought by the right pallial vein has passed through the right renal organ. Most of the blood probably passes back again to the auricles at their diastole, but a little

passes by a small vessel to the basi-branchial sinus and goes to the ctenidia (fig. 14). The latter vestigial vessel is probably the homologue of the very large efferent renal sinus of the right organ. The circulation is probably similar in other genera with a papillated sac (see Ainsworth Davis and Fleure for *Patella*). It is curious and difficult to understand. It might have some connection with preventing regurgitation to the ctenidia at systole, or with excretion, or with a newly acquired lymphatic function.



TEXT-FIG. 30. Living cells of left renal organ. ×750.

Histology of the Papillæ (fig. 33 and Text-fig. 30). The epithelial cells of the papillæ are tall and large and have very long vibratile cilia, which contrast with the very short ones of the cells of the right renal organ (fig. 32). They are particularly long towards the tips of the papillæ and create a strong current towards the lumen of the sac.

This is easily seen when papillæ are removed and placed in sea-water with a few specks of carmine (Text-fig. 30). The papillæ are sufficiently transparent for a good deal of the structure to be seen in slightly crushed papillæ and in teased preparations, after vital staining. The cells easily discharge their contents during fixation, but in fresh cells there are small pale yellow granules encircling the nucleus and very large colourless inclusions. The former stain vivid red and appear crushed together after vital staining with neutral red, whereas the latter stain with trypan blue. In sections these appear to have left empty vacuoles. When frozen sections are treated with Scarlet R., however, only a few fat or lipoid dots can be identified. There is practically no iron. In all respects the inclusions differ from those of the right renal cells. The cell walls are even more indistinct than those of the ordinary renal epithelium and it is difficult to separate the cells by usual dissection methods, but when separated they have irregular lobes which dovetail into those of adjacent cells (Text-fig. 30). In sections there are only radial striations between the cells (fig. 33). This leads to the suggestion that they form a syncytium. The nuclei vary in position according to the activity of the cells. They are smaller and stain much more darkly in sections than those of the right renal cells. Another difference is that no plastin nucleolus is present, although there are several karyosomes. The papillæ can be seen to discharge spherical globules with colourless inclusions to the lumen of the sac, as in the right renal organ. The free border can be seen to bulge up prior to this excretion, which probably contains uric acid, as positive reactions are given for the contents of the sac with appropriate tests. Perrier and Cuénot described the cells as small, probably because they had discharged their contents. Between the secretory cells, mucous cells and occasional phagocytes are wedged. The former have curious parallel spindles

similar to those found discharging from the mucous cells of the hypobranchial glands. Sometimes few of these cells are present, but in frequent specimens the spindles are in great quantities in the excretory fluid (Text-fig. 30). These are secretory spindles, varying from 0·01 mm. to 0·04 mm. in length, which Perrier Cuénot and Fleure have called crystals. These investigators tested them with micro-chemical tests for metallic salts and for proteins. Perrier thinks that the crystals are nutritive protein reserve, possibly albumen crystals. Cuénot concludes that their reactions do not contradict the possibility that the crystals are protein, but thinks they pass away with excretion. It is impossible to confirm these ideas from my observations. Mucin would probably also give positive reactions for protein. When left in sea-water these spindles swell up in the same way as those of the hypobranchial glands, and they stain with the usual mucin tests.

In the centre of each papilla there is a large lacunar space which seems always distended with blood cells, often pressed closely against the proximal part of the epithelium. Perrier describes a mesh of connective tissue cells between the epithelium and the lacunæ of the papillæ, but Cuénot states that it is entirely missing. There are a few widely separated connective tissue cells flattened against the epithelium (fig. 33, *c.t.n.*).

Cuénot and Pelseneer found amœbocytes penetrating between the epithelial cells, often reaching near the surface. These authors found that, eleven hours after physiological injection of Indian ink or sepia, numerous particles had been taken up by these phagocytic cells and from this they conclude that the left renal organ has taken on a special phagocytic blood function. The amœbocytes are certainly present, have dense granular cytoplasm which shows up in grey against the transparent cytoplasm of the epithelial cells and have migrated

almost to the surface of the papillæ (Text-fig. 30 and fig. 33, *ph.*). They frequently have long pseudopodia and take up solid particles after physiological injection, but the phagocytes are not so numerous as one would imagine from Cuénot's statements and figures. Any substance injected intravenously gets into the circulation and passes very rapidly to the lacunæ of the papillated sac, in fact, after injection to demonstrate the arterial system, these channels always fill up before any others, but it is difficult, unless the physiological injection is very weak, to show that the particles are actually taken up by the phagocytes. Cuénot and Pelseneer are probably correct in their conclusion that the papillated sac has special phagocytic activity. After physiological injection of suspended carmine, small particles are seen in the amœbocytes. Their observation that the phagocytes take up crystals from the internal parts of the epithelial cells and transfer them to the cavity of the sac seems to be entirely mistaken. Undoubtedly, however, the papillated sac retains some renal function, for globules containing colourless inclusions are seen discharging into its cavity. The fluid excreted contains more mucin and I find that the rate of excretion from the left renal opening into collecting tubes is much slower than from that of the right renal organ. It still retains reduced depuratory activity, but has probably two or three additional functions.

PHYSIOLOGY OF THE RENAL ORGANS AND OF ACCESSORY EXCRETORY STRUCTURES.

Many structures take part in excretion in *Haliotis*. In addition to the renal organs, the auricular fringes, the cells of the pericardial wall, the accumulative plasmatic cells and the digestive gland have excretory activity.

The right renal organ is undoubtedly depuratory and its epithelial cells excrete nitrogenous substances passed to them by the blood of the renal lacunæ, which comes from all parts of the body, and by the accumulative

excretory plasmatic cells, which are very abundant in the connective tissues of this renal organ. The excretion contains uric acid, as is shown by its reaction with Folin's test, and no urea reaction is given. Uric acid is, of course, usual in the excretion of Gastropods, as was first shown by Jacobson, in 1828.

There is forcible expulsion of fluid from the right renal organ, which is easily shown by passing a catheter through the renal opening. Probably this organ helps in the removal of surplus water, but probably the auricular fringes, or pericardial glands of Grobben, aided by heart pulsation, are very important in this connection, and, I think, possibly are not otherwise concerned in excretion. (See Heart, and fig. 15.)

The special cells of the ventral and lateral pericardial walls have acid vacuoles and are probably concerned in the excretion of uric acid (Text-fig. 21). The pericardial fluid is more acid than the excretion of either renal organ and gives positive reaction to tests for uric acid. The fluid excreted by the left renal organ and the pericardial fluid is carried to the exterior by the ciliary current set up by the powerful cilia of the papillæ of the left renal organ. This strong ciliary current of the papillæ has not been described by others. During heart pulsation the wall of the papillated sac is pushed forwards and this probably helps the outpush of the contents of its cavity. Although Bourne and others consider that the papillated sac has lost its renal function in the Haliotidæ, Pleurotomaridæ and Turbidæ, my evidence points to some retention of depurative function. The reaction of its excretion to uric acid tests is as definite as with the excretion of the right renal organ and the discharge of globules with vacuoles of watery fluid is actually seen in living papillæ, and the blood cells in their lacunæ have large acid vacuoles. The organ has doubtless assumed an additional phagocytic activity. The method of

physiological injection, commenced by Kowalevsky, for the determination of the function of the Molluscan renal organs, shows that phagocytes of the papillæ are capable of selecting solid basic particles, such as ammonia carmine, from the blood plasma, whereas the epithelial cells of the right renal organ are capable of eliminating acid substances in colloidal solution, such as indigo from picro-indigo carmine. Therefore the right renal organ alone has typical depurative function. The peculiar connection of the circulation of the left renal organ with the bases of the efferent ctenidial vessels is puzzling and may point to phagocytic activity or possibly to prevention of regurgitation of blood to the efferent ctenidial vessels.

The accumulative plasmatic cells, often 15μ in diameter, filled with inclusions, pass their excretory products to the cells of the right renal organ, and the cells of the digestive glands with coloured oily globules probably also take part in excretion (Text-figs. 23 and 19).

REPRODUCTIVE SYSTEM.

(Figs. 11, 17, 20, 29, 38, and Text-fig. 31.)

Haliotis is diœcious, but there is no sexual dimorphism and no copulatory organ or accessory glands.

The single gonad is remarkable for its simplicity. The genital products in both sexes escape to the cavity of the right renal organ (Text-fig. 22). They are freed into the sea through the renal aperture, where the ova sink and the spermatozoa swim. Fertilisation is left to the chance of helping currents, as in many primitive Gastropods and in Lamellibranchs. Cuvier stated that *Haliotis* is hermaphrodite, but I have found no evidence that it is hermaphrodite at any period. There has been more confusion about the genital organs in Rhipidoglossa than in any group of Gastropods.

In *Haliotis* the genital organ, in both male and female, opens by a simple longitudinal slit in the roof of the central part of the right renal organ. (*Vide* Right Renal Organ and fig. 29, *g.o.*) The orifice can be found in mature specimens at any time of the year, although Perrier and Von Jhering thought it was closed except during the spawning period. There is no genital duct and the opening is far removed from the external renal opening. According to my observations, the cavity of the gonad has lost the archaic connection with the pericardial cœlom. (See Cœlom.)

The original pair of genital glands has been lost, as in even the most primitive Gastropods. The gonad is developed very extensively on the right side of the body, but it is doubtful if this represents a fused pair of glands. The gonad forms a large part of the superficial region of the visceral mass in mature specimens, especially during the spawning months, but the extent varies much according to age. Fleure suitably points out that the gonad always develops at places which permit of free growth at breeding time, without alteration of the general shape of the body. It forms a complete superficial covering to the digestive gland, which is particularly well developed on the conical appendage; it also extends to the left of the large shell muscle and on the central parts of the visceral hump, where it overlaps other visceral organs (fig. 20). During, or just prior to spawning, it leaves uncovered only small parts of the digestive gland, stomach, renal organs and pericardium, and often forms a sheath half an inch in depth, so that the shell is prevented from shutting down. In mid-winter it is only a thin sheet of "spent" gonad.

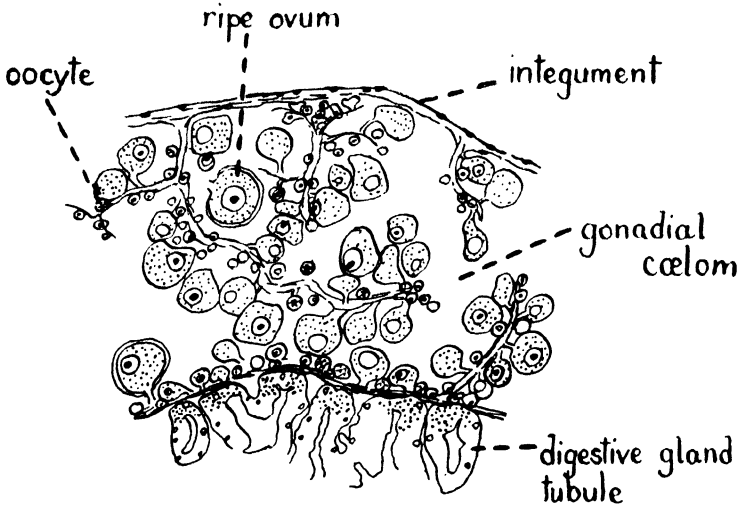
The only macroscopic difference in the two sexes is in the colour of the gonad, and this difference is more striking during the spawning period. The male gonad is cream to white, with frequent addition of green streaks, which also show when the gonad is cut open; very rarely there

are salmon or yellow tinges. When ripe the spermatozoa are in a milk-white fluid, which discharges in such quantities, through the shell perforations, that it imparts milkiness to a considerable surrounding area of sea-water. The female gonad varies from yellow-grey and green-grey to green. The pink colour, which Fleure mentioned as indicating sexual maturity, is probably due to the colour of the seaweed eaten, since it may be found any time of the year. As Stephenson has pointed out, it is often possible to tell the sex of *Haliotis*, from 4 cm. long upwards, without removal of shell, merely by pressing down the foot and epipodium on the right side and looking under the conical appendage, although the gonad colour is sometimes masked by tegumentary pigment.

The Histology of the Genital Gland is best seen in sections of specimens from 15 mm. to 25 mm. long, because in older specimens the very reduced gonocœle is bulged with genital products which mask the structure. The gonad is an arborescent racemose gland. The cœlomic epithelium, together with fine strands of underlying connective tissue, grows out in thin folds which may unite and form trabeculæ between the overlying connective tissue of the digestive gland and the integument. The epithelial cells produce either oogonia or spermatogonia (Text-fig. 31). *Haliotis* measuring 12 mm. to 20 mm. in length were the smallest in which ova showed differentiation in transverse sections.

Oogenesis can be followed but the chromosomes are small and difficult to count. During the growth phase the ova are attached to the trabeculæ by delicate stalks. When full grown they measure about 180μ in diameter. The cytoplasm is very densely filled with yolk granules and is surrounded by a vitelline membrane. The ova are ripe when freed into the gonad cœlom ; they pass via the right renal organ to the exterior. In male specimens spermatogenesis can be followed, but the spermatocytes

are very small. In sections of specimens which are about to spawn, streaming lines of fully developed spermatozoa are seen. They are of usual elongated type with a narrow head, to which clear vesicles of protoplasm are attached, and a long vibratile tail. They measure 18μ in length, including the tail. The number of spermatozoa and even of ova is extremely great.



TEXT-FIG. 31. T.S. of conical visceral appendage to show ovarian trabeculæ with oocytes and ova. ×45.

There is no evidence, even in the earliest stages of the gonad, of change of sex. As Stephenson has pointed out, female specimens are more numerous than males, but this applies to specimens of all ages. Stephenson found it particularly noticeable in the youngest specimens in which the gonad could be sampled. From specimens of all ages, during the summer, he had seventy females to fifty males; from specimens of marketable size, also in summer, I had fifty-nine females to thirty-nine males. Sexually mature *Haliotis* are about 5 cm. in length. Stephenson's observations show that the female gonad may be visible in specimens 2·5 cm. long and that spawning

occurs in females 5·5 cm. long; the male gonad is not recognisable until animals are 4 cm. long, but active spermatozoa are obtained in gonad samples of specimens 2·8 cm. long, and the male may spawn before it is 5·5 cm. long. He estimated that both male and female can spawn at three years old, "more likely at two years," but this is merely a suggestion from animals examined during May to early August. My observations are also in many ways too incomplete to give a definite idea of the age of spawning animals, but they range from March to the end of September of two years, with an additional summer, and much smaller post-larval stages were found than before. These measured from 2 mm. in length. The observations point to spawning occurring not earlier than at three years old. (Also see Growth Rate.)

Spawning Period of Haliotis is of doubtful duration. In the English Channel it may be from Spring to late Autumn. Stephenson says the breeding period is probably late Summer and there is no indication of a second breeding period in early Spring, as specimens only a few millimetres long are not found during Summer. I have found such specimens in July, August and September and also in March and April and, in the measurements of over four hundred specimens, there are no size gaps to indicate one brief spawning period. Spawning undoubtedly occurs at the end of July, during August and up to the third week in September, since I have observed spawning in the sea during these months in five individuals, and in frequent specimens spawning has occurred after collection. Stephenson recorded spawning in captivity at the beginning of August, but Wegmann's record for July and August at Roscoff, 1884, appears to be the first authentic record of spawning.

Spawning probably continues into late Autumn and the small specimens found in March and April may be the result. To account for the very tiny creeping stages

found in Summer, spawning possibly begins in Spring. Active spermatozoa have been found in the cavity of the right renal organ in March and April, but spawning has not been observed in Spring. As the length of larval life is unknown, it is impossible to come to any definite conclusion.

The Method of Spawning is the same for both sexes. The genital products are shot out, in successive clouds, through the shell perforations. The greatest quantity appears to pass out of the second and third oldest pores. In the spawning male there are puffs of white at intervals of three or four minutes regularly for about three-quarters of an hour. The puffs pass upwards and spread out so that the surrounding water for a circle quite three feet in diameter is milky. In one case the white cloud was first seen and the spawning male was found hidden in it. The ova make a grey-green cloud, which is not so conspicuous. They are puffed up to the surface and then sink. They do not adhere by mucin of the hypobranchial gland as Cuvier supposed and they are in countless numbers. I saw specimens draw down the shell immediately before each puff. Pressure of the shell on the visceral mass probably assists the spawning process. The mantle tentacles were seen to protrude through the shell pores in the interval between the puffs. They moved about and gave one the impression of clearing the holes. All five naturally spawning *Haliotis* observed were stationary during spawning, which occurred as the tide commenced to flow and on a warm sunny day. It is interesting that two spawning "ormers," found on top of rocks covered by about six inches of water, were the only ones ever found on upper surfaces. The number of spawning "ormers" seen is not sufficient to give an idea of the possibility of lunar periodicity. After spawning the gonad did not show marked signs of being "spent," so possibly the same "ormer" spawns several times between Spring and Autumn.

DEVELOPMENT.

Boutan gives some account, including four figures, of the development of *Haliotis* in his valuable account of zygobranch ontogeny. Together with Patten's work on the embryology of the limpet, Boutan's observations form the basis of knowledge of zygobranch ontogeny. *Haliotis* is, however, mentioned chiefly for comparison with *Acmæa*, *Fissurella*, etc., and unfortunately Boutan's work leaves scanty information about the habits and anatomical details of the late larval and early post-larval stages. The length of larval life is unknown. Such information would have greater interest than the early stages, which appear to follow the typical phases for primitive Streptoneura.

In this Memoir it is intended only to give a brief outline of the known stages. I hope in a future investigation to elucidate further details of metamorphosis.

Segmentation is total, gastrulation is by epiboly and the blastopore closes, so that the mouth is a new invagination. Stephenson obtained trochospheres fourteen to fifteen hours after fertilisation and after forty-four to forty-six hours the larvæ were freed from the egg shell and started pelagic life. There was little change at the end of sixty-two hours, after which Stephenson was unable to continue the work. Boutan says the trochosphere is peg-top shaped, as in *Acmæa*, but the cilia of the velum are shorter and there are no special tufts. He cannot determine if the velum has an indentation, as in the later stages of *Fissurella*. Professor Garstang, in his interesting address on " The Origin and Evolution of Larval Forms," recalls the fact that the trochosphere of Zygobranchia is very primitive and closely resembles that of Polychæta. He points out that in both cases adult characters are not clearly differentiated until the beginning of post-larval benthic life, but in less primitive forms the veliger larva shows early development of Gastropod characters.

In *Haliotis* body flexure occurs in the normal Gastropod fashion—prior to torsion—and is probably due to conflict of pressure of the growing foot and shell, which interferes with the anal function of the pelagic larva, as Robert has suggested for *Trochus*. After the flexure the anus is directed forward like the mouth and the shell is nautiloid. Garstang shows that the nautiloid form is only suited to backward progression, and Boutan states that mechanical and physiological difficulties in the larva have probably brought about larval torsion. He believes that this is accomplished in *Haliotis*, as in *Acmæa*, in a very few minutes, but at a slightly earlier stage. This torsion, through 180°, results in the anus, with the developing respiratory chamber, becoming dorsal to the head instead of being wedged in ventral position between the compressed foot and rapidly growing shell. As Garstang says, the physiological advantage of the reversed position is as obvious in the pelagic larva as in the creeping adult Gastropod. It gives better respiration, easier removal of waste products and allows the head to retract for protection under the wide part of the shell. The effect of torsion on the respiratory arrangements of the adult has been described under Respiratory System and under Systematic Position.

POST-LARVAL CHARACTERS.

According to Boutan, the spiral twisting of the visceral mass with its enclosing shell is, in all instances, quite independent of larval torsion and is the result of the commencement of post-larval creeping locomotion. The equilibrium must need great readjustment when the metamorphosed larva sinks to the bottom and adopts this new type of locomotion. In *Haliotis* the larval shell is retained and this growing inverted nautiloid shell, with its contained visceral mass, would tend to be a drag on the creeping foot and would press against its posterior end, dropping over to one side. This would upset the balance

of the foot and shell axes and retard growth of the shell and visceral mass on the one side—the left side—in *Haliotis*, which has a dextral spiral twist. Rapid growth of the anterior region and right side would begin the asymmetry and spiral growth.

In *Haliotis* the shell and visceral mass become much flattened dorso-ventrally, probably because of the habit of creeping into small crevices beneath rocks. This habit I have seen in *Haliotis* which were only 2 mm. long. Possibly wave action may help in the flattening, which appears to extend to the region of inhibited growth on the left side. The result is an adult with almost all its visceral mass and shell in the last whorl of the spiral and with continuation of shell growth always anteriorly and to the right side. The individual character of the asymmetry of *Haliotis* has probably, therefore, arisen as a post-larval adaptation, giving mechanical and physiological advantages for its mode of life. In the earliest post-larval stage the mantle and shell are doubtless without incision. This incision is at first median, as in the corresponding stage of *Fissurella* and *Emarginula* and in *Haliotis* the perforations, which are a still later adaptation, are also at first median (Text-fig. 2). Both incision and perforation allow for separation of outflowing used water and excretion from the incoming respiratory current. The shell perforations are better suited to *Haliotis* than a simple slit, for, during its movements in suspended position, often close to the sea bottom, sand, etc., would collect inside the respiratory chamber through an incision, as Fleure pointed out. The row of perforations becomes gradually nearer the left side because of rapid growth on the right side only, and also because of great hypertrophy of the right shell muscle, which displaces the respiratory chamber to the left side.

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EXPLANATION OF PLATES

Reference Abbreviations.

a. = Anus.
abd.g. = Abdominal ganglion.
abd.l. = Abdominal lacuna.
abd.l.o. = Abdominal lacunar orifice to renal vessel.
aff.ct.n. = Nerve of afferent ctenidial vessel.
aff.ct.v. = Afferent ctenidial vessel.
aff.+ren.n. = Nerve supplying afferent ctenidial vessel and renal opening.
aff.ren.v. = Afferent renal vein.
am. = Amœbocyte.
am.g. = Granular amœbocyte.
ant.ao. = Anterior aorta.
ant.ped.n. = Anterior pedal nerve.
ao.pe.n. = Aortic and pericardial nerve.
ao.tr. = Aortic trunk.
aur.ap. = Auricular appendages.
aur.c. = Cavity of auricle.
aur.l. = Left auricle.
aur.r. = Right auricle.
aur.ven.a. = Auriculo-ventricular aperture.
aur.ven.v. = Auricular ventricular valve.
b.br.s. = Basi-branchial sinus.
br.g. = Branchial ganglion.
br.p. = Branchial partition dividing posterior region of respiratory chamber.
bri. = Sensory bristles.
buc.a.a. = Anterior buccal arteries.
buc.g. = Buccal ganglion.
buc.n. = Buccal nerve.
buc.œs.n. = Bucco-œsophageal nerve.
buc.p. = Buccal glandular pocket.
buc.w. = Buccal wall.
C. 2 and 20 = Constrictor muscles of odontophore.
c.co. = Cerebral commissure.
c.g. = Cerebral ganglion.
c.p. = Shell pore, the most recently closed.
c.p.s. = Closed pore on shell spire.
c.ped.c. = Cerebro-pedal connective.
c.pl.c. = Cerebro-pleural connective.
c.t.n. = Nucleus of connective tissue cell.
c.t.s. = Connective tissue sheath.
cœc.gu. = Gutter of stomach cæcum.
cœc.gu.p. = Posterior gutter of cæcum.
cart.d. = Dorsal cartilage.
cart.l. = Lateral cartilage.
cart.v. = Vestigial anterior ventral cartilage.
ceph.a.s. = Cephalic arterial sinus.
ceph.ao. = Cephalic aorta.
ceph.p. = Cephalic pleat.
ceph.p.n. = Nerve of cephalic pleat.
ceph.ped.v.s. = Cephalo-pedal venous sinus.
ceph.t. = Cephalic tentacle.
ci.ep. = Ciliated epithelial cell.
con.a. = Conical appendage of viscera, which fits into pocket of mantle.
cr. = Crop.
cr.a. = Arteries of crop.
crys.l. = Crystalline lens.
ct. = Ctenidium.
ct.l. = Left ctenidium.
ct.r. = Right ctenidium.
cu. = Cuticle.
D. 1*a* and 4 = Dilatator muscles of odontophore.
d.c. = Diagonal out-going current of respiratory chamber.
d.gl. = Digestive gland.
d.gl.ant. = Anterior lobe of digestive gland.
d.gl.con. = Conical appendage of digestive gland.
d.gl.d. = Duct of digestive gland.
dia. = Dialyneury, or anastomosis of pallial nerve with visceral cord.
e.c.n. = Nucleus of excretory plasmatic cell.
e.ct.n. = Efferent ctenidial nerve.
e.gl. = Excretory globule of cell of right renal organ.
e.mem. = Basal (elastic) membrane of radula.
e.mem.c. = Cut edge of basal membrane of radula.
e.mem.r. = Ridge of basal membrane of radula.
e.mem.t. = Tip of basal membrane of radula.
e.pal.n. = External pallial nerve.
e.pal.n.l. = Left external pallial nerve.
e.pal.n.r. = Right external pallial nerve.

eff.a. = Aperture of right pallial vein to efferent ctenidial sinus.
eff.b. = Aperture of pericardial vessel to efferent ctenidial sinus.
eff.c. and *eff.d.* = Apertures of vessels of left renal organ to efferent ctenidial sinus.
eff.ct.s. = Efferent ctenidial sinus.
eff.ren.v. = Efferent renal vein.
eff.ren.s. = Efferent renal sinus.
end.i. = Incomplete endothelium.
ep. = Epipodium.
ep.a. = Anterior end of epipodium.
ep.d.f. = Dorsal fringe of epipodium.
ep.h. = Epipodial hillock.
ep.n. = Epipodial nerve.
ep.n.1. = Anterior epipodial nerve.
ep.t. = Epipodial tentacle.
ep.v.f. = Ventral fringe of epipodium.
ep.w.s. = White spot on ventral side of epipodium.
f.b. = Fibrous bridge.
g. = Gonad.
g.c. and *d.gl.* = Cut edge of gonad and digestive gland.
g.cœ. = Gonocœle.
g.n. = Genital nerve.
g.o. = Orifice of gonad to right renal organ.
gan.c. = Ganglion cell.
gan.c.f. = Fibril of ganglion cell.
gen.hep.a. = Hepato-genital artery.
gen.hep.v. = Hepato-genital vein.
gr. = Cytoplasm granules.
gv. = Longitudinal groove of pedal ganglion cord.
i.pal.n. = Internal pallial nerve.
i.pal n.an. = Anastomosis of internal pallial nerves.
int. = Intestine.
int. 1 and 2 = First and second limbs of intestinal loop.
int.a. = Intestinal artery.
int.e. = Intestinal epithelium.
int.g. = Groove in lymphoid tissue left by removed intestine.
int.l. = Intestinal loop.
int.ven. = Portion of intestine surrounded by ventricle.
integ.vis. = Visceral integument.
j. = Jaw (mandible).
kar. = Karyosome.
L. 11 and 12 = Muscles controlling lateral movements of odontophore.
l.pe.n. = Left pericardial nerve.
l.ren. = Left renal organ (papillated sac).
l.ren.c. = Cell of left renal organ.
l.ren.l. = Lacuna in wall of left renal organ.
l.ren.o. = External opening of left renal organ.
l.ren.p.c. = Left reno-pericardial canal.
l.ren.pap. = Papilla of left renal organ.
l.ren.v. = Vessels of left renal organ.
l.t. = Lymphoid tissue.
lab.co. = Labial commissure.
lab.n. = Labial nerve.
lac. = Lacuna.
m.ex. = Extrinsic muscles of odontophore.
m.f. = Muscle fibres.
m.in. = Intrinsic muscles of odontophore.
m.l. = Longitudinal muscles.
m.tr. = Transverse muscles.
mant. = Mantle.
mant.f.d. = Double mantle edge enclosing shell margin.
mant.l.r. = Anterior right lobe of mantle.
mant.l.l. = Anterior left lobe of mantle.
mant.o. = Oblique termination of mantle pocket.
mant.pl.m. = Muscle attaching mantle plate to visceral hump.
mant.pl.teg. = Junction of ventral mantle plate and visceral integument.
mant.pl.v. = Ventral mantle plate.
mant.t. = Pallial tentacle.
met.i. = Metaplasmic inclusions.
muc.c. = Mucous cell.
muc.c.c. = Ciliated cell of mucous gland.
muc.c.e. = Empty mucous cell.
muc.c.g. = Mucous cell of granular type.
muc.gl. = Mucous gland.
muc.gl.l. = Left mucous gland.
muc.gl.r. = Right mucous gland.
n. = Nucleus.
n.a. = Nucleus of amœbocyte.
n.a.d. = Dividing nucleus of amœbocyte.
n.cœl.e. = Nucleus of cœlomic epithelial cell.
n.f. = Nerve fibre.
n.œs. = Narrow part of œsophagus.
O. 1, 2, 3, 4 = Orifices of ducts of digestive gland.
o.c. = Out-going current of respiratory chamber.
o.p. = Oldest unclosed shell hole.

od. = Odontophore.
od.n. = Odontophore nerve.
œs. = Œsophagus.
œs.a. = Œsophageal artery.
œs.p. = Œsophageal pouch.
œs.p.a. = Artery of œsophageal pouch.
œs.p.l.o. = Opening of left œsophageal pouch.
œs.s. = Venous sinus of œsophagus.
œs.v.d. = Dorsal œsophageal valve.
œs.v.v. = Ventral œsophageal valve.
opt.a. = Optic artery.
opt.n. = Optic nerve.
opt.n.b. = Branch of optic nerve.
os. = Osphradium.
os.n. = Osphradial nerve.
P. 5, 9, 9*a*, 10, 10*a*, 17 = Protractor muscles of odontophore.
pal.a.m. = Median pallial artery.
pal.v. = Circular pallial vein.
pal.v.l. = Left anterior pallial vein.
pal.v.o. = Opening of pallial vein to abdominal hæmocœle.
pal.v.r. = Right pallial vein.
pap.l. = Lacuna in papilla of left renal organ.
pe. = Pericardium.
pe.c. = Cut edge of pericardial wall.
pe.c. and *r.ren.w.* = Cut edge of pericardial wall and wall of right renal organ.
pe.cœ. = Pericardial cœlom.
pe.ren.n. = Reno-Pericardial.
ped.a.i. = Posterior (internal) pedal artery.
ped.co. = Pedal ganglion commissure.
ped.cd. = Pedal ganglionated cords.
ped.d. = Dorsal surface of foot.
ped.ep.a. = External pedal and epipodial artery.
ped.ep.a.a. = Anterior pedal and epipodial artery.
ped.gl.a. = Anterior pedal gland.
ped.gl.p. = Posterior pedal gland.
ped.gl.s. = Pedal gland venous sinus.
ped.n. = Pedal nerve.
ped.s.a. = Anterior pedal sinus.
ped.s.p. = Posterior pedal sinus.
ped.so. = Pedal sole.
ph. = Phagocyte.
pig.l. = Pigment layer of retina.
pig.str. = Dorsal pigmented stripe of tentacle.
pl.ped.m. = Pleuro-pedal ganglion mass.
plas. = Plasmosome.
R. 1, 9*a*, 15, 18, 19 = Retractor muscles of odontophore.
R 1, *R* 2, *R* 3, *R* 4 = Two anterior and two posterior lobes of right renal organ.
r.pe.n. = Right pericardial nerve.
r.ren. = Right renal organ.
r.ren.o. = External opening of right renal organ.
r.ren.t. = Lumen of tubule of right renal organ.
rad. = Radula.
rad.c.e. = Extremity of radular cæcum.
rad.cæ.b. = Origin of radular cæcum from buccal cavity.
rad.s. = Radular sheath.
rad.s.n. = Nerve of radular sheath.
re.gr. = Refractive granules.
rect.a. = Rectal artery.
rect.n. = Rectal nerve.
rect.v. = Rectal vein.
ren.a. = Renal artery.
ren.c.u. = Renal cell bordering urocœl.
ren.int.a. = Reno-intestinal artery.
ren.n. = Renal nerve.
resp.c. = Respiratory cavity.
ret.c. = Retinal cell.
ro. = Rods secreted by retinal cells.
S. 3, 6, 7, 8, 13, 14, 16 = Shaping muscles of odontophore.
S. 21 = Sphincter muscle.
s.gl. = Salivary gland.
s.gl.n. = Salivary gland nerve.
s.gl.o. = Salivary gland orifice.
sen.c. = Sensory cell.
sen.c.n. = Nucleus of sensory cell.
sh. = Shell.
sh.f. = Flange on left side of shell aperture.
sh.m.a. = Artery of hypertrophied shell muscle.
sh.m.l. = Reduced left shell muscle, or its shell scar.
sh.m.n. = Nerve to right shell muscle.
sh.m.r. = Hypertrophied right shell muscle, or its shell scar.
sh.m.s. = Venous sinus of right shell muscle.
sn. = Snout.
sph.m. = Sphincter muscle.
st. = Stomach.
st.cæc. = Stomach cæcum.
st.g.co. = Stomato-gastric commissure.
st.gu. = Stomach grooves.
stat. = Statocyst.
stat.l. = Statolith.
stat.n. = Static nerve.
su.c. = Supporting cell.
su.c.n. = Nucleus of supporting cell.

sup.œs.visc.	= Supra-œsophageal visceral connective.
t.a.	= Tentacular artery.
t.n.	= Tentacular nerve.
t.œs.n.	= Tegumentary-œsophageal nerves.
teg.a.	= Tegumentary artery.
teg.n.	= Tegumentary nerve.
tr.b.	= Cytoplasmic inclusion stained with trypan blue.
typh.	= Typhlosole.
ur.	= Urocœle.
V	= Valve of cephalic arterial sinus.
V. 1, *V.* 2, *V.* 3	= Valves of stomach.
v.l.	= Venous lacuna.
ven.	= Ventricle.
ven.c.	= Cavity of ventricle.
ven.w.	= Cut wall of ventricle.
visc.a.	= Visceral artery.
visc.a. 1 and 2	= First and second visceral arteries.
visc.a. 1*d*	= Dorsal branch of first visceral artery.
visc.a. 1*v*	= Ventral branch of first visceral artery.
visc.co.l.	= Infra-œsophageal (pretorsional left) visceral cord.
visc.co.r.	= Supra-œsophageal (pretorsional right) visceral cord.
visc.m.v.	= Median visceral vein.
visc.sp.	= Visceral spire.
y p.	= Most recently formed shell hole.

All the drawings are of *Haliotis tuberculata*. The sections were drawn with the aid of projection apparatus.

Plate I.

Fig. 1. A young active living animal (shell 4·5 cm. long), drawn under dissecting lens. The arrows indicate the out-going current of the respiratory chamber, which passes out of the shell holes. × $\frac{2}{3}$.

Fig. 2. Ventral view of older living animal, which has been placed shell downwards in a pool, seen swinging its pedal-epipodial mass in preparation for turning over to clinging position. × $\frac{1}{2}$.

Fig. 3. The same specimen in process of heaving over to clinging position.

Fig. 4. The same specimen, which has just completed heaving over.

Fig. 5. *Haliotis* creeping in normal suspended position. The arrows indicate the direction of the incoming respiratory currents and the out-going diagonal current. (Compare Fig. 1.) × $\frac{1}{3}$.

Fig. 6. Part of the epipodium, to show the sensory structures. × $\frac{1}{2}$.

Fig. 7. Internal view of shell. × $\frac{1}{2}$.

Plate II.

Fig. 8. General dissection of digestive system. The buccal cavity, œsophagus, crop and stomach have been cut along their mid-dorsal lines. The dorsal part of the gonad has been removed to expose the digestive gland. *T.S.*—A, shows position of transverse section on Plate VIII. × 1⅓.

Fig. 9. (*T.S.*—B). Transverse section through œsophagus and radular apparatus, cut in the position shown by connecting line to Fig. 8. × 8.

Fig. 10. (*T.S.*—D). Transverse section cut through posterior end of œsophageal pouches, as shown by connecting line with Fig. 8. × 8.

Fig. 11. (*T.S.*—J). Transverse section passing through crop, stomach and stomach cæcum, in position shown by connecting line to Fig. 8. × 8.

Compare these transverse sections with those on Plate VIII, which are of the same specimen (shell 18 mm. long).

Plate III.

[*T.S.*—C, F, G, K, indicate positions of transverse sections in Plate VIII.]

Fig. 12. Dorsal view of specimen 5 cm. long, with shell removed and vessels carrying oxygenated blood injected in red. The nerves are black lines. The pericardium only is opened. × 1½.

Fig. 13. Dissection of the heart. The pericardium, auricles, ventricle and left renal organ (papillated sac) have been opened to show the various apertures. × 1½.

Fig. 14. Injected specimen dissected from the ventral surface. Part of the foot, epipodial muscular mass and shell muscle have been removed. Vessels carrying oxygenated blood are shown in red and the arterial portions are cross-hatched; vessels and sinuses carrying de-oxygenated blood are uncoloured. × 1.

Fig. 15. Living appendages of auricle (pericardial gland of Gröbben), containing amœbocytes. These were stained vitally with trypan blue and neutral red. Drawn with camera lucida. × 700.

Fig. 16. Living blood cells. Drawn with the aid of camera lucida. × 700.

Plate IV.

[*T.S.*—E (*a* and *b*), *T.S.*—H, indicate positions of transverse sections in Text-fig. 24 and Plate VIII.]

Fig. 17. Dorsal view of general dissection of injected animal. Part of the œsophagus has been removed to show the odontophore mass and the cephalic arterial sinus. The mucous gland, roof of the pericardium and right renal organ are removed; part of the right ctenidium and the right auricle are displaced to the left. Vessels carrying oxygenated blood are shown in red; those of the arterial system are cross-hatched, but those carrying de-oxygenated blood are uncoloured. × 1⅓.

Plate V.

Fig. 18. Dorsal view of radular apparatus. The pharyngeal roof and ventral wall of œsophagus have been removed and the basal (elastic) membrane is cut in the middle line and lifted back on the right side to show the supporting cartilages and musculature of the odontophore. × 3.

Fig. 19. Ventral view of mouth and odontophore muscles, showing relative position of nerves. × 3.

Fig. 20. General dissection of nervous system from the dorsal side. The respiratory chamber has been opened on the left side and its roof displaced to the right. The visceral mass has been removed from the pedal and right shell muscular mass and the latter has been cut away to dissect the pedal ganglionated cords. × 1¼.

Plate VI.

Fig. 21. Dorsal view of pleuro-pedal ganglion mass and proximal parts of nerves and connectives. The suspension of the statocysts by three muscular strands, the static nerves and the orifices of the pedal arteries and venous sinuses are also shown. × 9.

Fig. 22. Part of a transverse section of the right statocyst, passing through the static nerve. The epithelial cells lining the cavity are only shown near the static nerve. Few of the many statoliths are shown. Camera lucida. × 700.

Fig. 23. Dorsal view of living right statocyst and part of the left one, with surrounding connective tissue sheath. The nerve cells and fibres have been stained vitally with methylene blue. Camera lucida. × 35.

Fig. 24. Median longitudinal section of eye protuberance of animal 4 mm. long. Camera lucida drawing. × 200.

Fig. 25. Transverse section passing through osphradium and osphradial nerve. Camera lucida drawing. × 200.

Fig. 26. Extended tentacle of living animal (2·5 cm. long). × 20.

Fig. 27. Transverse section of cephalic tentacle. Camera lucida. × 150.

Fig. 28. Longitudinal section of two papillæ of tentacle stained with iron-hæmatoxylin and orange G. Camera lucida drawing. × 650.

Plate VII.

Fig. 29. Dissection to show the extent of the four lobes of the right renal organ. The central part of the ventricle is cut out to show the opening of the left reno-pericardial canal. The right ctenidium and the rectum are displaced to the left. × 1⅛.

Fig. 30. Horizontal section of small *Haliotis* (6 mm. long) passing through respiratory chamber, pericardium, both renal organs and the external opening of the right renal organ. Camera lucida drawing. × 15.

Fig. 31. Horizontal section of older animal (23 mm. long) passing through the external opening of the left renal organ, through the left reno-pericardial canal and through the ventricle surrounding the intestine. Camera lucida drawing. × 12.

Fig. 32. Tubule and part of the epithelium bordering the urocœle of the right renal organ. Camera lucida. × 650.

Fig. 33. Section cutting a papilla of the left renal organ longitudinally. The epithelial cells and the central lacuna are shown. Camera lucida drawing. × 650.

Plate VIII.

Fig. 34. (*T.S.*—A). Transverse section, passing through buccal opening, cut at the position shown in Fig. 8. The specimen (18 mm. long) is the same one as in the sections on Plate II. × 8.

Fig. 35. (*T.S.*—C). Transverse section of the same specimen, passing through the cephalic arterial sinus, in the region where the pedal arteries pass from it by a valved orifice. The position of the section is shown in Fig. 14. × 8.

Fig. 36. (*T.S.*—F). Transverse section of the same specimen cut in a more posterior position, as shown in Fig. 14. The cephalo-pedal venous sinus is shown, with the partition dividing it from the cephalic aorta. × 8.

Fig. 37. (*T.S.*—G). Transverse section of small specimen (7·5 mm. long) passing through the middle region of the respiratory chamber. It shows the attachment of the growing edge of the shell to the reduced left shell muscle. The position of the section is shown in Fig. 12. × 16.

Fig. 38. (*T.S.*—H). Transverse section of older specimen (23 mm. long) passing through the posterior end of the respiratory chamber, hypertrophied shell muscle and conical visceral appendage. The position of the section is shown in Fig. 17. × 5.

Fig. 39. (*T.S.*—K). Transverse section of the same animal as in *T.S.*—A, C and F, passing through the pericardial region and posterior visceral mass. It shows the position of the ventral mantle plate. The position of the section is shown in Fig. 14. × 8.

The sections on this Plate and on Plate II show the torsion of the œsophagus.

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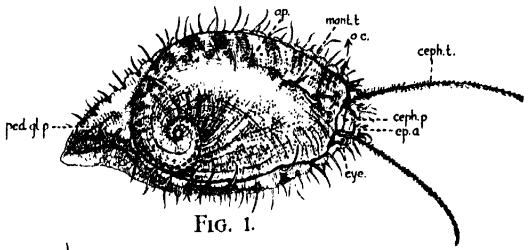
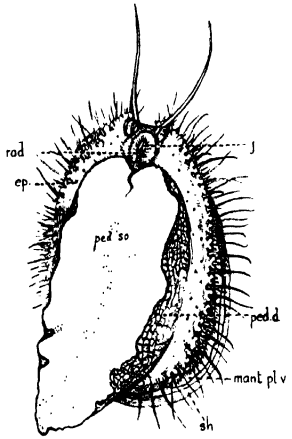


Fig. 1.



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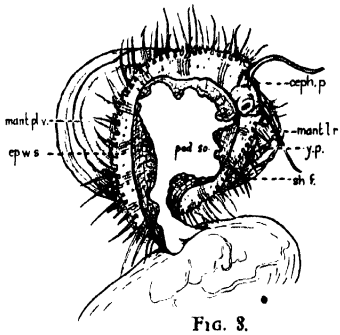

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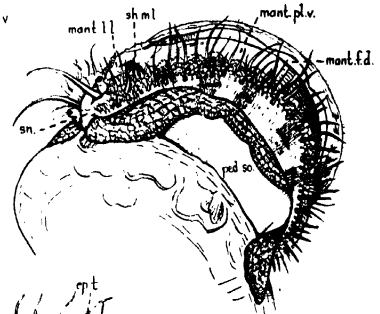

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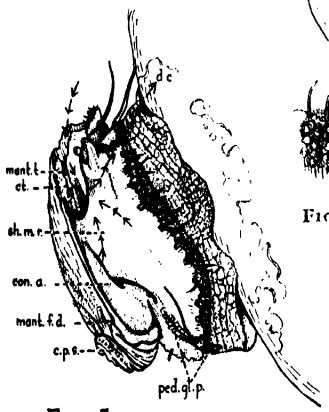

Fig. 5.

Fig. 6.

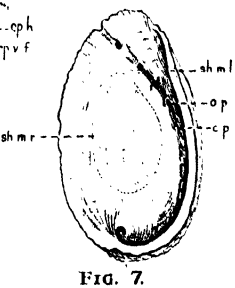

Fig. 7.

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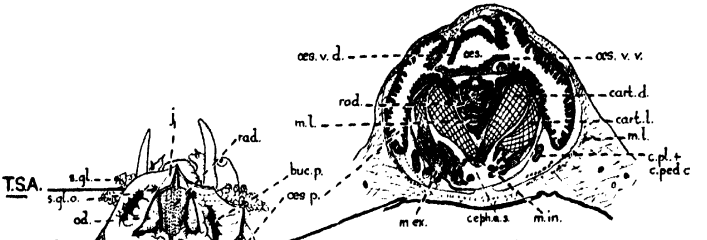

FIG. 9 (T.S.B.)

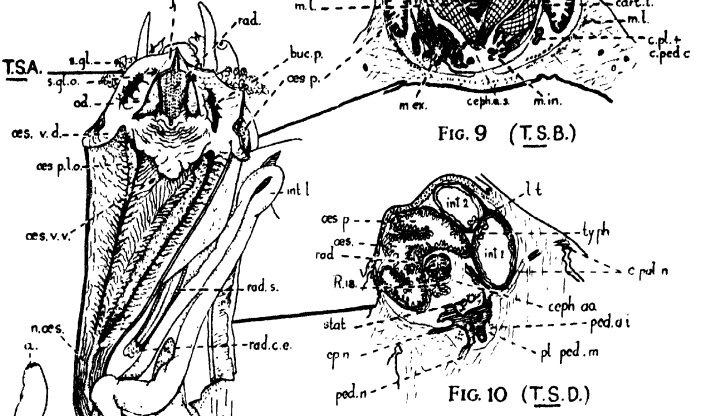

FIG. 10 (T.S.D.)

FIG. 8

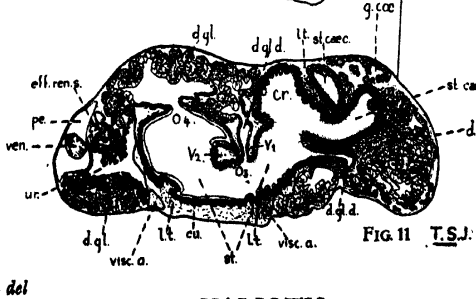

FIG. 11 T.S.J.

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HALIOTIS

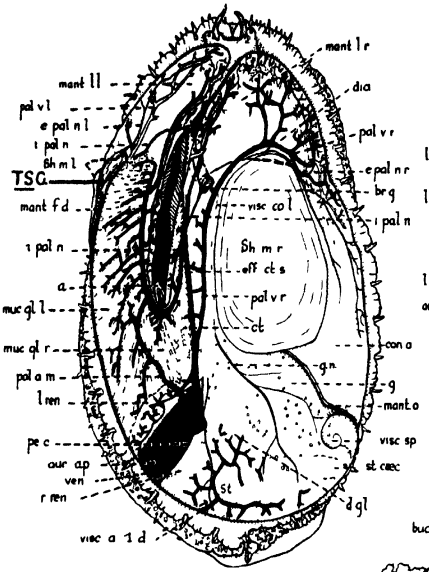
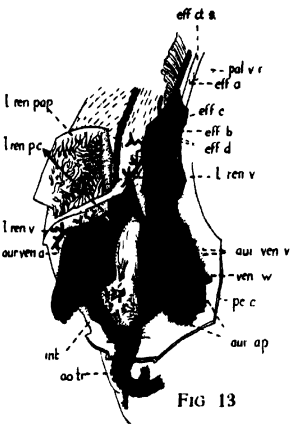


FIG. 12



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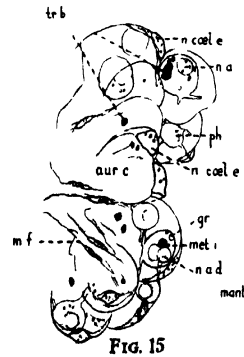

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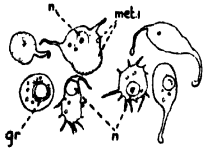

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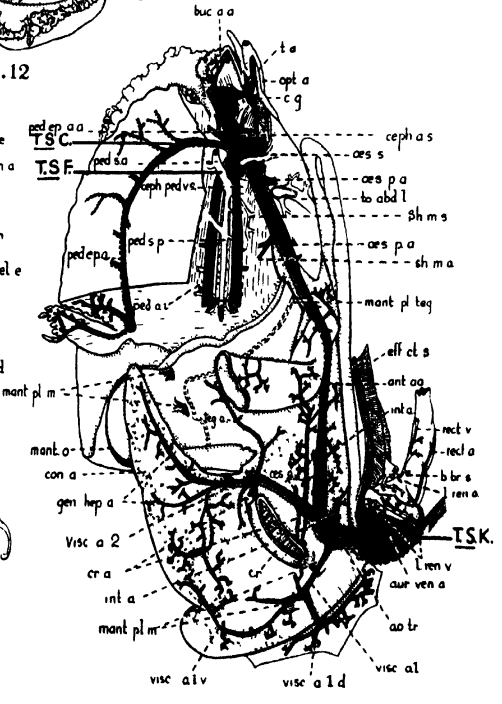

FIG. 14

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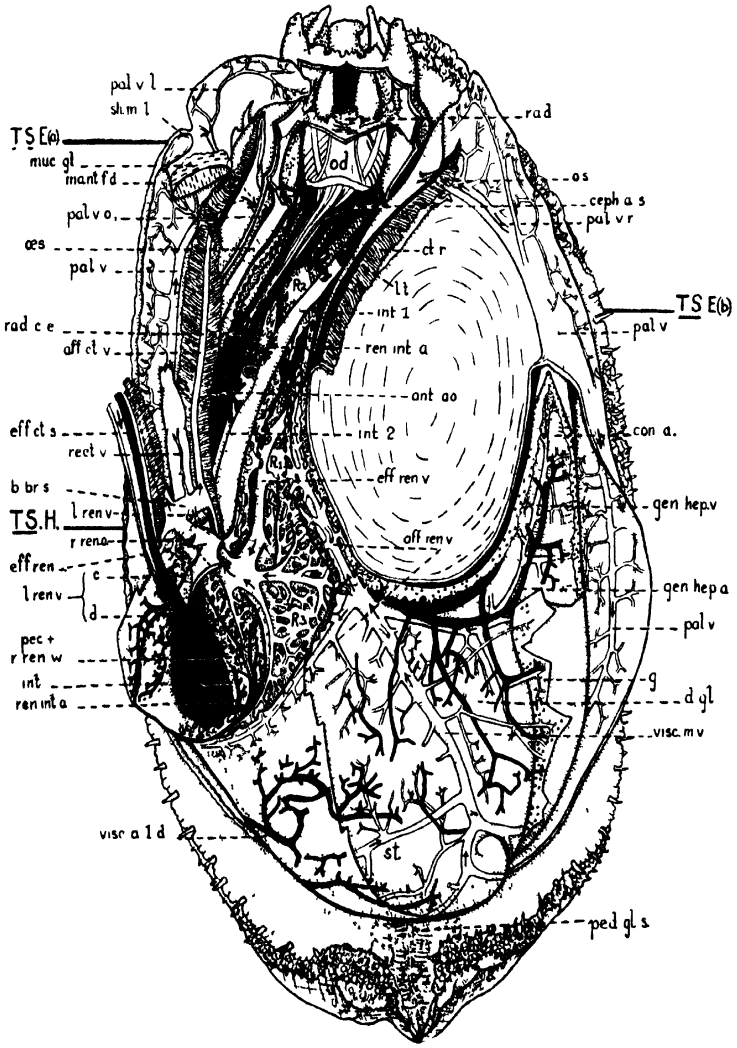

FIG. 17.

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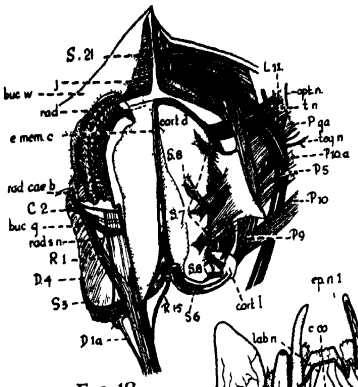

Fig 18

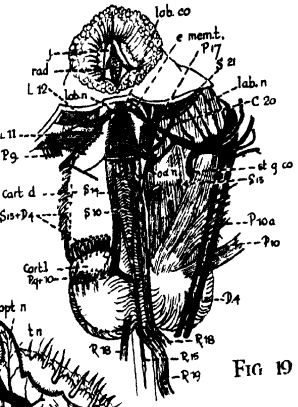

Fig 19

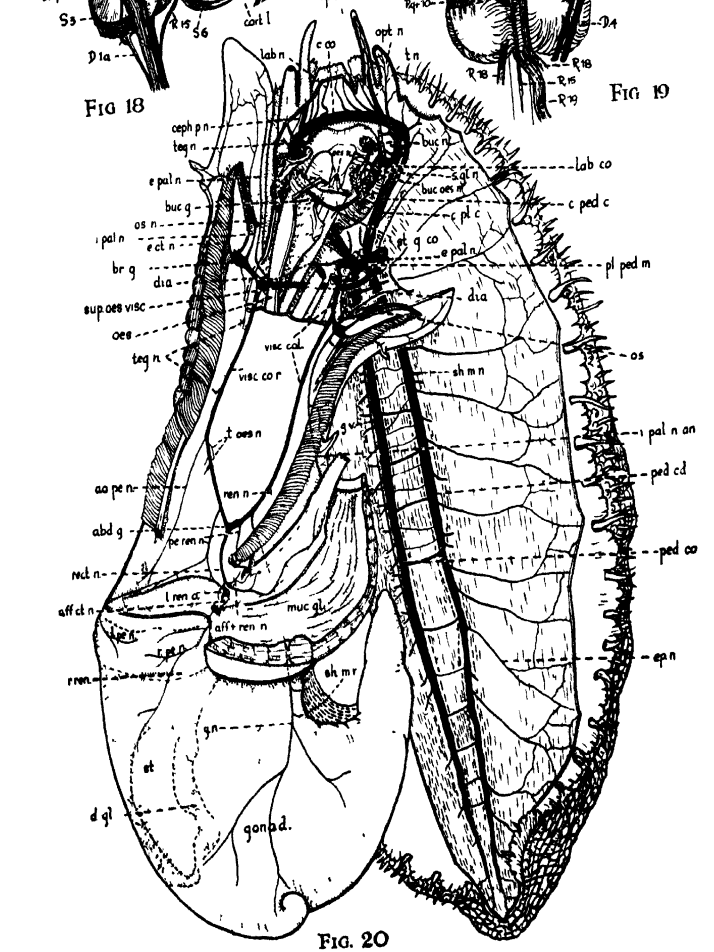

Fig. 20

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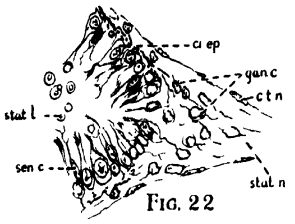

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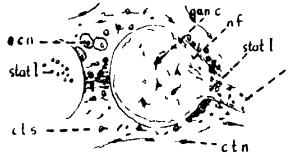

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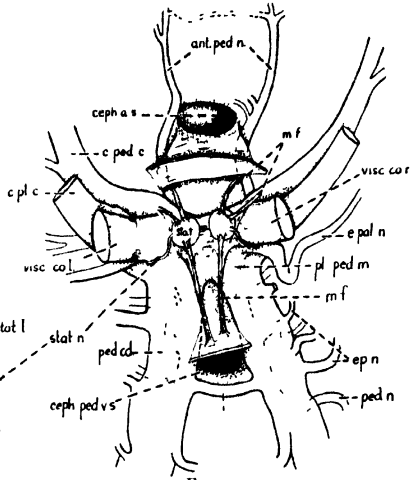

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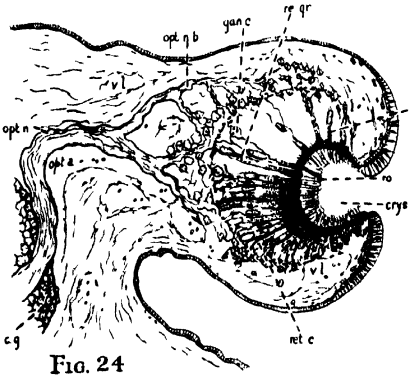

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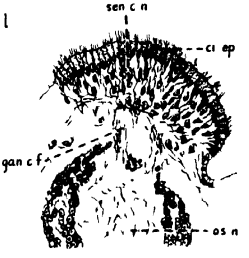

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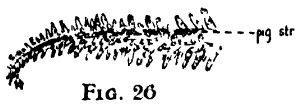

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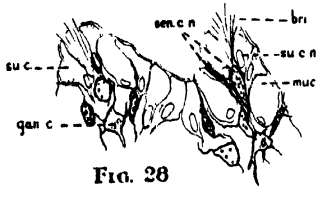

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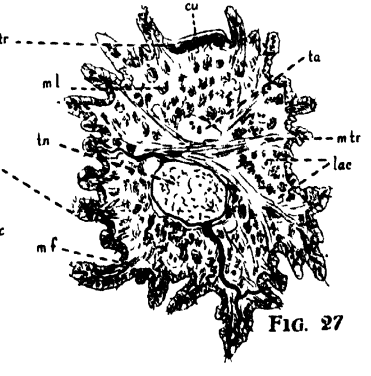

FIG. 27

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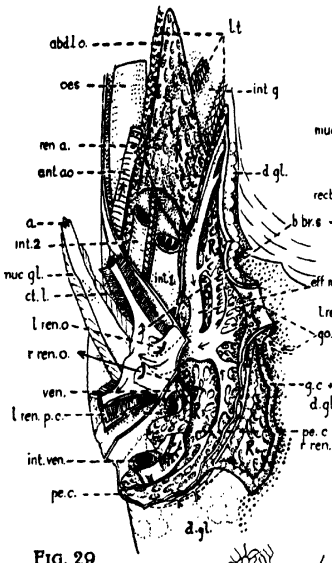

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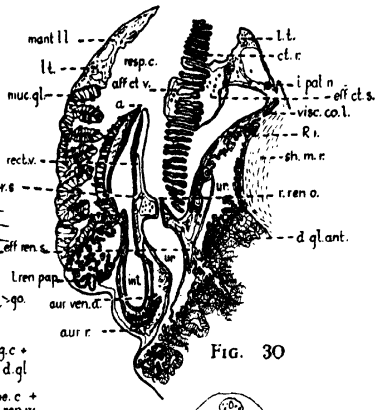

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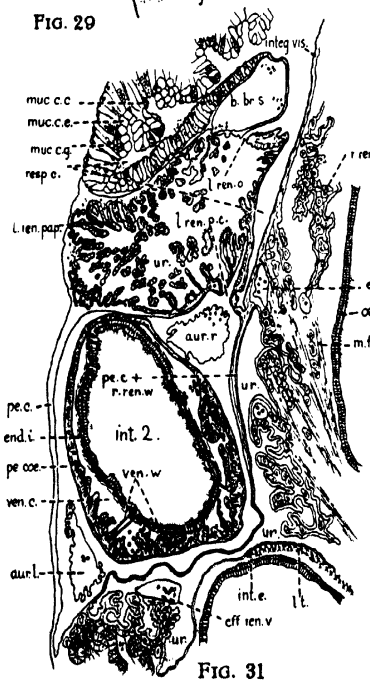

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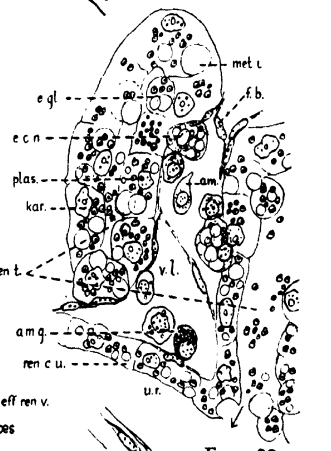

Fig. 32

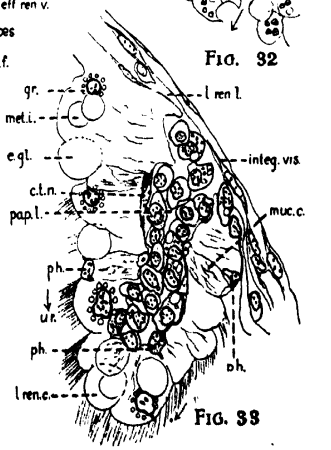

Fig. 33

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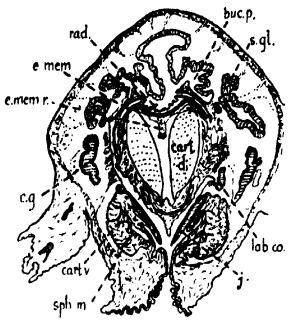
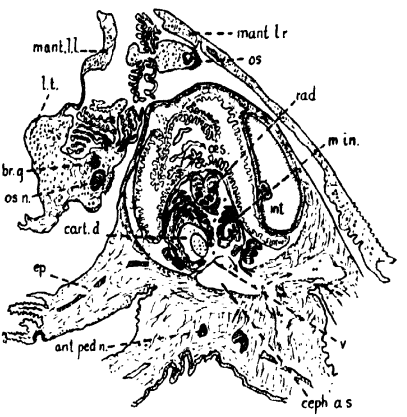


Fig. 34. (T.S.A.)



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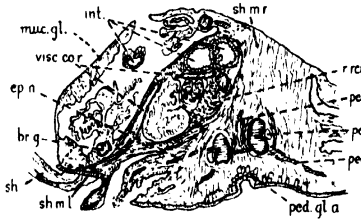

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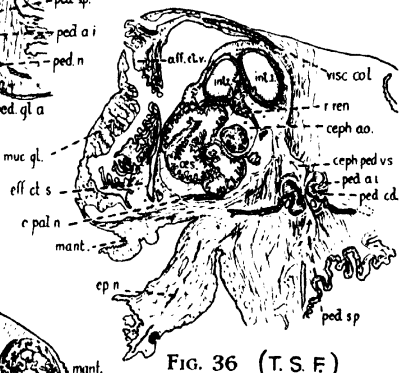

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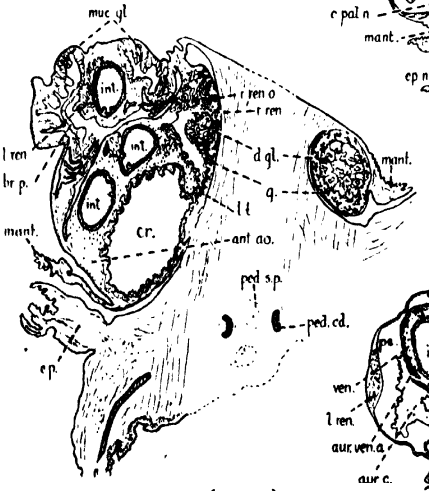

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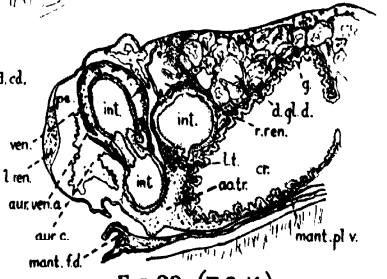

Fig. 39. (T.S.K.)

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